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THE FOREST FORMATIONS OF BOULDER COUNTY, COLORADO

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(WITH TWELVE FIGURES)

The present paper purposes to describe the forest formations of the eastern slope of the Rocky Mountains in Boulder County, Colorado. There has been a large amount of work done on the flora of Colorado from the systematic and distributional standpoint, the results of which are contained in RYDBERG'S *Flora of Colorado* (Bull. 100, Colorado Agricultural College Experiment Station, 1906). In the publications of the Forestry Bureau, U. S. Department of Agriculture, and the U. S. Geological Survey, there are a few papers treating of the economy (and incidentally the ecology) of the forests of the state; while a popular paper by RAMALEY ("Remarks on the distribution of plants in Colorado east of the divide") appeared in *Postelsia* for 1901, in which is given a considerable mass of data on the distribution and ecology of the plants of this region; but as yet there has been done no work of an exact character in the determination of the physical conditions under which the forests exist. For this reason I hope that the following discussion will prove of value.

The discussion will cover the following points: introduction, being a brief account of methods employed and a short description of the physical features of the region studied; composition of the forests with reference to the controlling and most common secondary species, and the relationship between them; physical character of the habitat with reference to water content of the soil, temperature of air and soil, humidity, light, pressure (altitude), slope, and expo-

sure; past and present extent of the forests and their present movement, including deforestation and reforestation. The time spent in the investigations upon which this paper is based includes the summers of the years 1902 to 1905 inclusive. [1]

Introduction

The methods which I have employed are given in detail in a recent work, *Research methods in ecology*, by DR. F. E. CLEMENTS, and are therefore treated here very briefly. They include the use of a Draper psychrograph and thermograph, a geotome, aneroid barometer, maximum, minimum, and ordinary thermometers, egg-beater psychrometers, and a simple photometer.

A set of the Draper instruments was established in Boulder, at an altitude of 1620^{m}, and at timber-line on the east slope of the Continental Divide at an altitude of about 3420^{m}. A set of records of these instruments was taken between June 21 and July 20, 1905. The instruments were set each week by comparison with a watch and with the humidity and temperature readings obtained from the egg-beater psychrometer and the thermometer. The thermograph records were found to agree within a few degrees with the temperature as given by the thermometer, but very little confidence can be placed in the psychrograph records as the reading recorded by this instrument seldom, if ever, tallied with the readings given by the hand psychrometer, and in fact the two psychrographs when running side by side did not agree with each other closer than seven per cent.

A set of maximum and minimum thermometers was placed at the mouth of a small cañon at an altitude of 1710^{m} and readings taken weekly from June 23 to July 31, 1905. From August 4 to September 4 these were stationed on a moraine in open pine timber at an altitude of 2550^{m}. Another set was kept on the open plains three miles east of Boulder at 1590^{m} altitude from the middle of June to the end of September.[2]

With the geotome, two soil cores were obtained at each station, one of the first 11.25^{cm}, and one from 11.25 to 22.5^{cm} in

[1] See below.

[2] The thermographs and psychrographs were elevated about 1.2^{m} above the ground, the maximum and minimum thermometers 0.6^{m}. They were all carefully housed so as to protect them from the sun and yet afford free access to the air.

depth.[3] These readings are of course not entirely satisfactory in determining the soil water available for the trees, with their roots extending to a depth of many feet; but the deeper sample probably

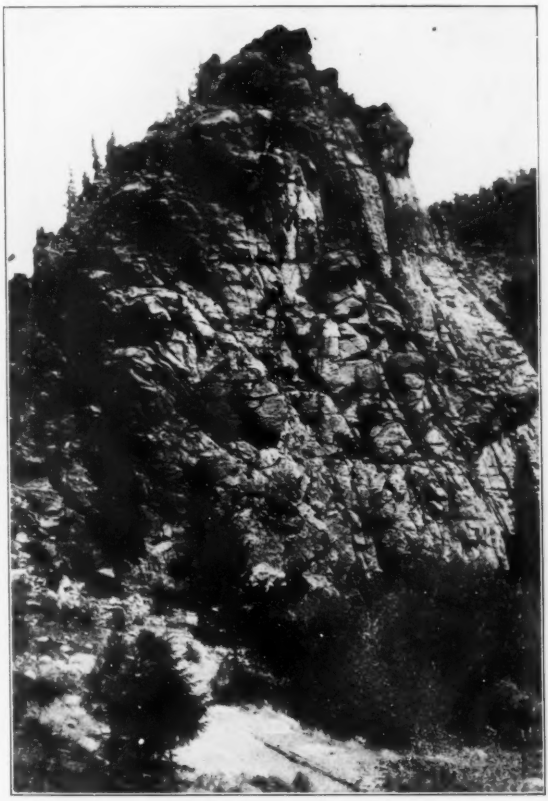


FIG. 1.—Castle Rock in Boulder Cañon, altitude 2250m; in the foreground and to the right is seen the Populus angustifolia–Salix Nuttallii formation; scattered over the hills are Pseudotsugas and Piceas.

gives a fair basis for comparison of habitats in this respect. It is exceedingly difficult in any extended investigation to carry a geotome which will reach a depth of several feet. The soil samples obtained

[3] Exceptions to these depths will be noted below.

with the geotome were carried to the laboratory in Boulder in tightly closed tin cans and weighed as soon as possible after collection. They were then opened, the samples dried for three days at an average temperature of 24 to 29°C., after which they were weighed again. The difference between the two readings gave the weight of moisture contained in the soil, and this weight is expressed in per cent. of weight of the dried sample. In the case of soil samples which it was necessary to carry in the pocket for several days before weighing, an allowance of a few decigrams must be made, since there was a slight evaporation from the tins. This slight inaccuracy, however, is not sufficient to invalidate the general results.

At each station soil temperatures were taken on the surface of the ground and at depths of 11.25^{cm} and 22.5^{cm}, respectively. The air temperature was taken at 7.5^{cm} and 9^{dm} above the ground; while humidity readings were also taken at 7.5^{cm} and 9^{dm} above the surface. Occasionally humidity and temperature readings at 1.8^{m} above the ground were taken.

The light readings in each formation were obtained with the photometer, and these were evaluated in terms of a standard series of ten readings of one to ten seconds respectively, taken at 12:30 P. M. on October 2 at 1620^{m} altitude in Boulder. A similar series was taken at noon on June 23, but unfortunately lost.

The aneroid barometer was used in obtaining the approximate altitudinal limits of the formations, and the altitudes so obtained were checked whenever possible by those obtained by the United States Geological Survey.

The observation stations were chosen at points as nearly typical as possible for each formation, and at most stations from three to many observations were taken during the summer of 1905.[4] Where the formations showed isolated societies within their limits, separate stations were selected for each of these.

Boulder County, Colorado, lies on either side of the fortieth parallel of north latitude. Its western boundary is the Continental Divide of the Rocky Mountains, while to the east it extends about 19^{km} from the base of the mountains. With the exception of the banks of streams on the plains, the forested area is confined to the mountains,

[4] Three observations were taken in 1907 as noted below.

which were originally pretty heavily timbered; but since the settlement of the region, the forests have been and still are disappearing. The topography of the mountains has been determined by vast elevation accompanied by extensive faulting, and followed by great erosion. The face of the country is exceedingly broken. High,

FIG. 2.—Foothills near Boulder; the altitude of the tops of the hills in the background is approximately 1950m; in the foreground is seen the shrub-grass formation of the foothills, which in this view is dominated by a grass-sagebrush society; scattered over the hills in the background is *Pinus scopulorum*.

rocky ridges alternate with deep cañons walled in by rocky precipices hundreds of feet in height, with an occasional granite dome isolated from the general mass. Such a dome is shown in *fig. 1*.

Passing from the plains westward toward the Continental Divide, we first encounter the foothill region of the main range (*fig. 2*). This is a region of broken ridges with steep slopes, cut at intervals of 1.5

to 7^{km} by larger and smaller cañons running from east to west, in which flow the streams. Extending north and south from these main cañons are numerous smaller cañons and gulches, so that the entire region is very irregularly furrowed in all directions. The foothill region is 6 to 8^{km} wide and at its summit reaches an altitude of about 2250^{m}, although some of its individual peaks may reach a height of 2700^{m}.

From the western end of the foothills to the base of the main range is a distance of about 16^{km}. This is the plateau region, ascending gradually from 2250^{m} to 3000^{m} at the base of the range. While the surface of this region is much broken, it is less so than either the foothills to the east of it or the main range to the west, and its general contour is comparatively even. In its eastern part, however, where the streams lie far below the general level, are found the deepest and most rugged parts of the cañons. In its western portion are many beautiful little parks along the stream courses (*fig. 3*) which afford good crops of hay and excellent pasturage. Above 3000^{m} the country again becomes much broken, the steep and rocky slopes encountered above timber-line culminating at the crest of the range in vast chasms and inaccessible pinnacles of rock. Above 2400^{m} the mountains have been extensively glaciated. The ice sheet at the time of its greatest extent covered all but the highest ridges above 2700^{m}, while tongues of ice in some places extended down to nearly 2400^{m}. As evidence of this condition we have today the vast morainal deposits, the chains of little glacial lakes (*fig. 4*), and the existence of a small glacier on the eastern slope of the Arapahoe Peaks some 32^{km} west of Boulder. The highest summits in Boulder County are Mt. Audubon and the Arapahoe Peaks, with approximate altitudes of 4050^{m}.

The principal streams are North, Middle, and South Boulder Creeks, Jim Creek, the North and South St. Vrains, and Left Hand Creek. All of these rise at the base of the range and flow eastward to join finally the North Platte River.

The climate of the region is semi-arid. At Boulder, situated directly at the base of the mountains, the average rainfall for nine years has been 42.7^{cm}. In the higher mountains there is a much heavier annual rainfall than this, the difference between Boulder

and the summit of the range being 25^{cm} in 1904. The rainfall at the base of the mountains occurs mainly in April and May, but in the higher mountains it is distributed through spring and summer.

FIG. 3.—A mountain "park" on Boulder Creek, 35^{km} west of Boulder; in the foreground are a few *Pinus Murrayana* and *Pinus scopulorum;* in the middle foreground is the upper extension of the Populus angustifolia–Salix Nuttallii formation intermingled with *Populus tremuloides* and Piceas; to the right is an aspen grove; on the mountain in the background is a burned area in Pseudotsuga and *Pinus Murrayana* timber, in the lower part of which are a few aspen groves.

The heavy snows of winter, packed in the ravines by the high winds, do not melt until late in summer and are the principal source of water for irrigation.

At the base of the mountains the temperature range is from 37°.7 to −34°.4, though neither of these figures is often reached by thermometers elevated a few feet above the surface of the ground.[5]

The following is the record of maximum and minimum temperatures obtained by me during the summer of 1905: At Boulder (1620^{m}) from June 21 to July 20 the maximum thermograph reading was 34°.4, the minimum 5°. At timber-line during the same period the maximum thermograph reading was 22°.2 and the minimum −3°.9. Three miles east of Boulder on the plains (1590^{m}) the maximum and minimum thermometers from June 13 to July 31 gave a maximum of 40°.3 and a minimum of 6°.1; from July 31 to August 31 a maximum of 41° and a minimum of 9°.7.[6] The instruments at the cañon mouth (1710^{m}) from June 13 to July 31 gave a maximum of 31° and a minimum of 7°.7, while those on a moraine (2550^{m}) from August 1 to August 29 gave a maximum of 30°.3 and a minimum of 4°.7. These results show an approximate difference in mean temperature of 11° between Boulder and timber-line, an approximate difference of 1° per 160^{m} altitude, the difference in the maxima being slightly greater and in the minima slightly less than this. It must of course be borne in mind in the study of these results that they are fragmentary, covering comparatively short periods.

As already remarked, comparatively little confidence can be placed in the psychrograph records. The curves traced by the two instruments are in no way conformable to each other, owing to the fact that the relative humidity is dependent on such local factors as sunlight and wind and hence is liable to sudden and considerable variations within limited areas. I have even known the temperature recorded by the wet-bulb thermometer to fall 1°.5 C. within a few seconds when a sudden breeze sprang up, succeeding a calm. These facts show that a comparison of humidity readings between different stations at any given instant of time is open to serious error, and even the readings of the dry-bulb thermometer may vary locally owing to local conditions.

In the following discussion I shall consider a "formation" as a

[5] All temperatures are recorded in degrees Centigrade.

[6] The great difference between the maximum at Boulder and three miles east of Boulder is doubtless traceable to the different elevations of the instruments above the ground at these points.

group of plants of definite composition as to species, occupying a definite habitat as to the physical characteristics of the latter, or a definite area as to geographical position. A "society" is a definite group of plants as to component species occupying a secondary position within a formation. The "characteristic species" of a formation are those which dominate the area occupied by that formation. Thus the "characteristic species" of the "cottonwood-

FIG. 4.—The Picea-Abies formation with a glacial pond in middle foreground.

willow formation" of the lower cañons and plains are *Populus occidentalis* and *Salix fluviatilis*. Within this "formation" we find the Crataegus and Corylus "societies."[7]

Composition of the forests

The forests of Boulder County may be classed under the following formations: (1) Populus occidentalis–Salix fluviatilis formation; (2) Populus angustifolia–Salix Nuttallii formation; (3) Pinus

[7] I have given these definitions for the sake of clearness, but with no claim of originality. The nomenclature of the paper is that used by RYDBERG (*op. cit.*).

scopulorum formation; (4) Pinus Murrayana formation; (5) Apinus flexilis formation; (6) Pseudotsuga–Picea Engelmanni formation; (7) Picea Engelmanni–Abies lasiocarpa formation.

While *Populus tremuloides* occupies numerous areas through the mountains, I have not thought best to consider it of higher rank than a society. My reason for denying it formational rank is that it occupies varying habitats, associating with the other formations, and never dominating areas which are well defined either as to their physical features or geographical position.

All these formations are montane excepting the first, and even this extends up the cañons to about 1950^{m}. The second, on the contrary, while chiefly montane, overlaps the first on the plains.

(1) THE POPULUS OCCIDENTALIS–SALIX FLUVIATILIS FORMATION (*fig.12*)

This formation occupies the banks of streams on the plains and, as already mentioned, is found also in the lower cañons. It is a straggling tree formation scarcely worthy the name of forest. While restricted mainly to the stream banks, groves of trees may occasionally be found along the borders of the old flood plains.

It is a very mixed formation, consisting essentially of two layers, an upper woody layer and a lower herbaceous one. The former may be divided into two subordinate layers, one controlled by *Populus occidentalis* and the other by *Salix fluviatilis*. These are not, however, usually coexistent, but alternate, the cottonwood controlling here and the willows there. Associated with the two characteristic species of the formation are many individuals of *Populus angustifolia*, but these do not control. A few scattered shrubs occur in the formation but are not sufficiently numerous to be considered as an independent layer (see below). The herbaceous layer, moreover, might be separated into two subordinate ones; but since its constituent forms present every gradation in height, such a separation would be entirely arbitrary and superficial. A ground layer of mosses and liverworts is occasionally present.

The formation is an open one. Occasionally the trees form a sufficiently dense growth to exclude all but the more shade-loving species, but for the most part they are separated by intervals of many

feet, thus permitting the entrance of a large amount of sunlight and admitting most of the species from the adjoining formations. These species are largely ruderal, owing to the presence of cattle and the proximity of farms and highways.

Of the weeds entering into the formation some of the commonest are *Medicago sativa, Melilotus alba, M. officinalis, Trifolium pratense, T. repens, Phleum pratense, Poa pratense, Bromus brizaeformis, Poly-*

FIG. 5.—The Populus occidentalis–Salix fluviatilis formation, two miles above the mouth of Boulder Cañon; to the left the control is shared by *Populus occidentalis* and *Rulac negundo;* to the right *Salix fluviatilis* dominates.

gonum lapathifolium, Verbascum thapsus, Ambrosia trifida, Solidago canadensis, and *Helianthus grosseserratus* (?).

In the more dense parts of the formation, the forms of the under layer are more sparse both as to number of species and number of individuals. Three of the more characteristic are *Anemone canadensis, Vagnera stellata,* and *Viola canadensis.*

The stream banks form a path along which some of the montane species are invading the plains. Hence we find in the cottonwood formation a few such forms as *Viola canadensis* and *Apocynum*

androsaemifolium. A few species from the adjoining plains are invading the formation. These include an occasional *Artemisia* sp. and a few individuals of *Festuca octoflora*. *Eleocharis palustris* wanders in occasionally from nearby meadows.

While the under layer of the formation is so mixed that it is difficult to assign a dominant rôle to any forms, yet in general it may be said that this layer is characterized by *Agrostis alba* and *Melilotus alba*. The vernal aspect is not derived from any species or group of species, the color of the vegetation at this season being mainly green. In its late aestival and autumnal aspect the yellow of Solidago and Helianthus gives to the vegetation its predominant color.

In the lower cañons (*fig. 5*) the formation maintains the loose straggling character which it presents on the plains. Here, however, an intermediate layer of shrubs forms one of the most important parts of the formation (*figs. 5, 6*). Chief among these are *Alnus tenuifolia* and *Corylus rostrata*. Other members of this layer are *Crataegus cerronis*, *C. coloradoensis*, *Clematis ligusticifolia*, *Ampelopsis pentafolia*, *Prunus americana*, *P. melanocarpa*, *Rosa pratincola*, and *Acer glabrum*. In the densely shaded thickets formed by these shrubs, the under layer is composed mainly of *Hydrophyllum Fendleri*, *Viola canadensis*, *Galium trifidum*, and *Vagnera stellata*. Species from the higher slopes occasionally wander in, such as *Berberis Fendleri* and *Prunus melanocarpa*.

In places where the light value falls as low as 5 : 300, the under layer is largely lacking.

Mixed as is this formation on the plains, in the narrow and steep-sloped cañons its continuity is still more difficult to follow. The species from the adjoining shrub-grass formation of the cañon sides come down to the bottom of the cañon and mingle with those of the cottonwood-willow formation, ruderals are numerous, and along the stream banks members of the brookside formation, such as *Collinsia parviflora*, *Mimulus minor*, and *Veronica peregrina*, are found. Wherever sandbars are formed by the shifting current of the streams on the plains, the cottonwoods, principally *Populus occidentalis*, are invading them in large numbers. Such invasions, for the most part, are only temporary, however, on account of the floods which in spring overflow these sandbars, destroying the plants on them.

Owing to the physical condition of the surrounding habitats, the Populus occidentalis–Salix fluviatilis formation is in a practically static condition. My data on the physical characters of the habitat of this formation are as follows:

Observations taken on Boulder Creek east of Boulder during July 1905 gave results as follows:

*Temperatures**

(Observations July 3, 11 A. M.; 10, 10:45 A. M.; 24, 11:15 A. M.; 28, 1:45 P. M.)

	−22.5cm	−11.25cm	0cm	+7.5cm	+9dm
Minima.....	16°2	16°	16°6	20°5	21°2
Maxima.....	20°25	18°5	31°25	26°5	25°5

*Zero indicates the ground surface, minus readings below surface, and plus readings above the surface.

Water content

Observations	11.25cm	22.5−11.25cm
July 10.....	30.1 per cent.	18.3 per cent.
July 24.....	8.8 per cent.	9 per cent.

Relative humidity

(Observations July 3, 11 A. M.; 10, 10:45 A. M.; 24, 11:15 A. M.; 28, 1:45 P. M.)

	7.5cm	9dm
Minima.....	43 per cent.	38 per cent.
Maxima.....	73 per cent.	60 per cent.

The light value in this formation taken above the under layer at noon on August 7 was 9 : 180.

In a thicket of *Corylus rostrata* at the mouth of Boulder Cañon, three series of observations gave the following results:

Temperatures

(Observations June 24, 10:15 A. M.; July 17, 12:20 P. M.; August 30, 7 A. M.)

	−22.5cm	−11.25cm	0cm	+7.5cm	+8dm	+1.8m
Minima.....	13°5	13°8	14°4	16°75	17°	17°5
Maxima.....	18°	18°	21°5	25°5	27°	27°5

Water content

Observations	11.75cm	22.5−11.25cm
June 24.....	29.5 per cent.	24.6 per cent.
July 17.....	12.5 per cent.	12.4 per cent.
Aug. 30.....	5.3 per cent.	7.2 per cent.

Relative humidity

(Observations June 24, 10:15 A. M.; July 17, 12:20 P. M.; August 30, 7 A. M.)

	7.5cm	9dm	1.8m
Minima.....	30 per cent.	27 per cent.	26 per cent.
Maxima.....	80 per cent.	83 per cent.	88 per cent.

In a hawthorn society at the mouth of a small cañon at an altitude of 1710^{m}, observations were made at three stations. One of these was in the center of the thicket, close to a small stream; this I shall designate as Station E. A second station, which I have called E_1, was chosen about midway between the center and edge of the thicket; and the third, or Station E_2, was taken just at the edge of the thicket. The results obtained for these three stations follow:

Temperatures

Station E (Observations June 12, 7 P.M.; 13, 6 P.M.; July 1, 8:15 A.M.; 8, 10:30 A.M.; 17, 9:10 A.M.; August 26, 9:45 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}	+7.5^{cm}	+9^{dm}	+1.8^{m}
Minima.....	14°.2	13°	14°	12°*	12° †	16° †
Maxima.....	19°	20°.75	25°	26°.5*	26°.5 †	28° †

* Five observations.
† Four observations.

Station E_1 (Observations June 13, 6 P.M.; July 1, 8:45 A.M.; 8, 11 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}
Minima.....	13°.6	13°.4	13°
Maxima.....	15°.2	15°.5	16°.8

Station E_2 (Observations June 13, 7 P.M.; July 1, 9:15 A.M.; 8, 11:15 A.M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}
Minima.....	14°.75	15°	14°.6
Maxima.....	17°.6	17°	19°.5

Water content

	Observations	11.25^{cm}	22.5−11.25^{cm}
Station E.....	June 14	22.8 per cent.	30.8 per cent.
	July 1	25.3 per cent.	33.3 per cent.
	July 8 (raining)	25.8 per cent.	35.6 per cent.
	July 17	11 per cent.	16.7 per cent.
	August 26	6.2 per cent.	9.6 per cent.
Station E_1.....	July 1	14.4 per cent.	15.4 per cent.
	July 8 (raining)	18.6 per cent.	13.3 per cent.
Station E_2.....	July 1	6.2 per cent.	13.3 per cent.
	July 8 (raining)	10.2 per cent.	16.3 per cent.

Relative humidity

Station E (Observations, June 12, 7 P.M.; 13, 6 P.M.; July 1, 8:15 A.M.; 8, 10:30 A.M.; 17, 9:10 A.M.; August 26, 9:45 A.M.)

	7.5^{cm}	9^{dm}	1.8^{m}
Minima.....	45 per cent.	42 per cent.	21 per cent.
Maxima.....	80 per cent.	77 per cent.	77 per cent.

Light value

Station E..... August 26 9:45 A.M. = 5: 300

(2) THE POPULUS ANGUSTIFOLIA–SALIX NUTTALLII FORMATION (*fig. 1*)

The transition between this and the preceding formation is a wholly gradual one, the narrow-leaf cottonwood occurring, as already noted,

as a secondary form in the preceding formation. The upper limit of *Populus occidentalis* is about 1950^{m}. At this altitude it is replaced by *Populus angustifolia*.

Like the preceding, this formation lacks continuity, the characteristic species only occasionally exercising control, and being interrupted in places by the Pseudotsuga-Picea formation. In scattered association with *Populus angustifolia* and *Salix Nuttallii* are *Alnus tenuifolia*,

FIG. 6.—A hawthorn society.

Betula fontinalis, *Acer glabrum*, and in the lower parts of the mountains an occasional *Salix Fendleriana*. These shrubs form a straggling society along the cañon bottoms and may be occasionally found running up the mountain sides in favored localities. Two under layers, one of flowering plants, the other of mosses, liverworts, and lichens, are usually present; but these layers, as well as the upper, lack continuity and are very open. The herbaceous, or middle layer, is very mixed and holds no definite level, owing to the varying height of its constituent species. The frequent presence of a highway in the

cañon is causing the invasion of this formation by various weeds the commonest of which is *Trifolium repens*.

Common species of the middle layer are *Geranium Richardsoni*, *Rudbeckia ampla*, *Aconitum columbianum*, *Aquilegia coerulea*, *Viola canadensis*, *Heracleum lanatum*, and *Vagnera stellata*. Occasionally a *Mertensia ciliata* from the brookside formation of the Hudsonian zone wanders down the cañons to 2250^{m}.

In the upper limits of the formation the cottonwoods are mainly absent, the control here being shared by *Salix Nuttallii* and *Alnus tenuifolia*, with an occasional invasion of *Pseudotsuga mucronata*, *Picea Engelmanni*, *Picea Parryana*, and *Populus tremuloides*. In these places the ground is usually very wet and there are present in the middle layers, in addition to the forms already enumerated, *Senecio triangularis*, *Trollius albiflorus*, *Thalictrum occidentale*, *Oxypolis Fendleri*, *Panicularia nervata*, *Carex variabilis*, *Montia Chamissonis*, *Carex canescens*, *Agrostis hiemalis*, and *Geum oregonense*. The middle layer here is usually open, but occasionally the grasses or Carices form closed societies.

The formation is in a static condition. Within the cañons at least there is no apparent migration of the cottonwoods taking place, though an occasional *Salix Nuttallii* has invaded the mountain slopes to a point outside the proper limits of the formation.

The observations made in a thicket of *Corylus rostrata* and those in a hawthorn society, and recorded under the Populus occidentalis formation, apply equally well to this formation, since these formations overlap at this point, as I have already mentioned. In addition ot these observations, I have three observations taken during the summer of 1907. These observations were made at three stations which I shall call A, B, and C respectively. Stations A and B were in Boulder Cañon about 20^{km} west of Boulder at an altitude of about 2250^{m}, while station C was at the mouth of Boulder Cañon. Station A was 6^{m}, B 6^{dm}, and C 1.2^{m} from the edge of the stream.

My observations follow:

Temperatures

		−75^{dm}	−15^{cm}	0	9^{dm}
Station A.	(June 26, 5 P.M.)	11°	13°	14°	
Station C.	(July 30, 5 P.M.)		16°.5	19°.2	21°.2

		Water content	
		15cm	17–75cm
Station A.*	(June 26)	43.7 per cent.	14.6 per cent.
Station B.*	(June 26)	30.0 per cent.	.....
Station C.†	(July 30)	21.2 per cent.	.....

* Observations made following a period of showery weather.
† Rain two days previous.

(3) THE PINUS–SCOPULORUM FORMATION (*fig. 2*)

This formation covers the dry slopes of the mountains from their base at an altitude of 1650m to about 2400m. It is exceedingly open, the pines seldom exercising any decided control on the surrounding vegetation, except when associated with the Douglas firs. While the Pseudotsuga characteristic of the Pseudotsuga-Picea formation extensively overlaps the Pinus scopulorum formation, I have thought best to consider the two as distinct, because the characteristic habitat of each is distinctly different. Pseudotsuga, in the lower part of its range, is restricted to the north slopes and the cañon bottoms, while *Pinus scopulorum* occurs indifferently over north and south slopes alike, and is absent from the cool, moist cañon bottoms (see below). *Pinus scopulorum* is frequently associated in more or less dense clumps with Pseudotsuga, and where such is the case, or where the pines themselves grow densely, there is present no under layer whatever, with the exception of a few mosses and lichens. As soon as the formation becomes thinned out a little, shrubs and grasses from neighboring areas wander in. *Sabina scopulorum* is found in scattered association with the pines throughout the formation.

According to old residents of the county, the pines were formerly much more numerous than at present, having been largely cut for timber, this species having been formerly the principal timber tree of the mountains. At present comparatively little is being cut. The formation is in a dynamic condition. Large numbers of pine saplings are springing up throughout its extent, and on the mesas, which extend peninsula-like from the mountains on to the plains, are numerous strips of open pine forest, gradually invading the grass land of the plains.[8] An exposed sandstone cliff 11km from the base of the

[8] RAMALEY (*op. cit.*, p. 31) explains the presence of trees on the west end of the mesas and their absence on the east end by a difference in moisture between the two. Since the pines grow on exposed south slopes of the mountains, however, where the water content is very low, this explanation does not appear to me fully satisfactory.

mountains at Boulder bears in a crevice a young specimen of yellow pine.[9] Occasionally *Celtis reticulata*, a representative of the eastern forests, is found invading this formation.

The absence of a secondary layer where the pines and Douglas firs grow densely is not to be explained alone on the ground of a scarcity of light or of moisture, but rather by the combined absence of these factors. The shade is seldom dense enough to exclude shade-loving plants, were sufficient moisture present to satisfy the needs of such forms.

The physical factors of this formation were taken at an altitude of about 2100^{m} on a north slope in a small grove of pines and Douglas firs. The results are given below:

Temperatures

(Observations July 29, 12:15 P. M.; August 14, 5:15 P. M.; September 13, 3:40 P. M.)

	-22.5^{cm}	-11.25^{cm}	0^{cm}	$+7.5^{cm}$	$+9^{dm}$
Minima.....	16°2*	19°*	18°75	21°75	22°
Maxima.....	17.25*	20°*	26°	27°	26°75

* Two observations.

Relative humidity

(Observations July 29, 12:15 P. M.; August 14, 5:15 P. M.; September 13, 3.40 P. M.)

	7.5^{cm}	9^{dm}
Minima.....	21 per cent.	23 per cent.
Maxima	65 per cent.	35 per cent.

Water content

Observations	11.25^{cm}	$22.5-11.25^{cm}$
July 29.....	3.7 per cent.	4.4 per cent.
August 14.....	3.6 per cent.	2.6 per cent.
September 3....	1.6 per cent.	2.1 per cent.

Light values

September 13..... 3:40 P. M. = 4 : 60 (in medium shade)
= 4 : 360 (in direct shade of tree trunk)

(4) THE PINUS MURRAYANA FORMATION (*figs. 7, 8*)

This formation replaces the Pinus scopulorum formation at about 2400^{m} altitude and stands between it on the one hand and the Apinus flexilis formation on the other, though it is overlapped by each of these, and indeed the two latter overlap each other at about this altitude. The question may be raised whether the *Pinus Murrayana* forests deserve recognition as an independent formation, or should be classed

[9] In this connection see also SHANTZ, "A study of the vegetation of the mesa region east of Pike's Peak: the Bouteloua formation." BOT. GAZETTE 17:185, 186.

as a part of one or both of the two just named. Since, however, they occupy a definite zone, between 2400 and 3000^{m}, only occasionally straying up to 3300^{m}, which zone is not coincident with that of either of the two others, I have decided so to consider them.

FIG. 7.—*Pinus Murrayana* and Pseudotsuga timber near Nederland, Colorado; approximate altitude 2550^{m}.

This formation occupies the dry mountain sides and is absent from the cañon bottoms. In the former situations it frequently mingles with the Pseudotsuga-Picea and Picea-Abies formations. Its habitat, however, is distinct from that of either of these. While this formation is much broken, alternating with the Carex-grass-shrub

formation of the moraines and with the numerous societies of *Populus tremuloides*, it is less open than either of the other pine formations of the mountains. In some places the trees are separated by an average interval of but a few decimeters, which is usually the case in the

FIG. 8.—Boulder Creek between Nederland and Eldora, approximate altitude 2490m; in the cañon bottom *Alnus tenuifolia* and *Salix Nuttallii* dominate; the cañon sides are clothed with a mixture of the Apinus flexilis, Pinus Murrayana, Pseudotsuga-Picea, Picea-Abies, and Pinus scopulorum formation.

younger groves. In the older forests there is ordinarily a greater interval between the trees. The normal abundance of the species in a forest formation in a region which has been burnt and timbered as extensively as have the mountains of Boulder County is obviously difficult to determine satisfactorily. But in comparison of apparently

virgin tracts of *A pinus flexilis* and *Pinus Murrayana*, I find that the latter grows more densely than the former. I know of no virgin tracts of *Pinus scopulorum*.[10]

In the denser parts of the formation the under layer is very scanty, and consists mainly of *Pyrola secunda*, *Arctostaphylos uva-ursi*, and *Chimaphila umbellata*, with a few mosses and lichens. Where the formation is more open frequent invaders from the neighboring Carex-grass-shrub formation straggle in. *Razoumofskya americana*

FIG. 9.—*Pinus Murrayana* and *Populus tremuloides* timber, two miles west of Sunset, Colorado; approximate altitude 2700m.

is a common parasite of *Pinus Murrayana*. Relative to the damage wrought by this and the preceding species of mistletoe see JACK (*op. cit.*, p. 45).

The discussion of the deforestation and reforestation of the areas included in this and the succeeding formations I shall reserve for consideration under "Succession."

Observations of the physical character of the habitat of this formation were taken at two stations. One of these was in a mixed

[10] In this connection see also JACK, Pike's Peak, Plum Creek, and South Platte Reserves, U. S. Geol. Survey, 20th Ann. Rep., pt. 5, p. 50.

forest of *Pinus Murrayana* and *Pseudotsuga mucronata* at an approximate altitude of 2550^{m}, with a northwest exposure. At this station three sets of observations were taken on July 13, 25, and August 29. The other station, at which but one set of observations was made on August 29, was in a grove of young pines on a northwest exposure at an approximate altitude of 2520^{m}. The first of these I shall call Station A, the second Station B.

Temperatures

Station A (Observations July 13, 10:50 A. M.; 25, 3:20 P. M.; August 29, 6:45 A. M.)
Station B (Observation August 29, 1:40 P. M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}	+7.5^{cm}	+9^{dm}
Minima.....	9°.6	11°	12°.5	14°.5	15°*
Maxima.....	13°	14°.5	26°	23°.25	20°.25

* Two observations.

Relative humidity

Station A (Observations July 25, 3:20 P. M.; August 29, 6:45 P. M.)
Station B (Observation August 29, 1:40 P. M.)

	7.5^{cm}	9^{dm}
Minima.....	43 per cent.	45 per cent.
Maxima.....	67 per cent.	64 per cent.

Water content

	Observations	11.25^{cm}	22.5−11.25^{cm}
Station A.....	July 25	9.8 per cent.	6.9 per cent.
	August 29	6.7 per cent.	9.5 per cent.
Station B.....	August 29	5.3 per cent.	4.2 per cent.

(5) THE APINUS FLEXILIS FORMATION

This formation occurs over the dry mountain slopes from 2550^{m} up to timber-line. In the lower part of its range it is represented by only a few scattering individuals, but above 3000^{m} it is the dominant pine formation. Here it extensively overlaps the Picea-Abies formation, but I have thought best not to classify it with the latter as Apinus-Picea-Abies formation, because it occupies as a rule higher, drier ground than the firs and spruces, which are found in the cañon bottoms as well as on the higher slopes.

Even in the virgin forest, the trees are separated by comparatively wide intervals, but their spreading tops meeting overhead produce a sufficiently dense shade to exclude all but a few straggling invaders from the open slopes, with the exception of the mosses and lichens and *Vaccinium microphyllum*, which form the characteristic layer of the forest floor. This last species forms a loose straggling layer in both this and the spruce-fir formation of the high mountains, attain-

ing a height of only a few inches. Biologically, the under layer of this formation is open, but the physical conditions of its habitat are such as to exclude most plants.

Save where artificial conditions such as fire or lumbering have intervened, the continuity of this formation is comparatively unbroken, except in its lower limits, where it is represented only by a few straggling individuals.

Observations of the physical character of the habitat of this formation were made at two stations which I designate as A and B. Station A was on a gentle slope with a southwest exposure, at an approximate altitude of 2940^{m}. Station B was on a comparatively level area at an altitude of approximately 3150^{m}. A series of three observations at these stations gave the following results:

Temperatures

Station A (Observations July 5, 1:45 P. M.; 27, 11:15 A. M.; September 5, 12 M.)
Station B (Observation July 19, 6:30 A. M.)

	−22.5^{cm}	−11.25^{cm}	0^{cm}	+7.5^{cm}	+0.9^{m}
Minima.....	5°8*	6°2	6°	11°‡	11°‡
Maxima.....	8°†	8°	13°4	14.5‡	13°75‡

* Depth of 17.5^{cm}. † Depth of 20^{cm}. ‡ Three observations.

Relative humidity

Station A (Observations July 5, 11:45 P. M.; 27, 11:15 A. M.; September 5, 12 M.)
Station B (Observation July 19, 6:30 A. M.)

	7.5^{cm}	9^{dm}
Minima.....	34 per cent.	27 per cent.
Maxima	63 per cent.	59 per cent.

Water content

	Observations	11.25^{cm}	22.5−11.25^{cm}
Station A.....	July 5	17.3 per cent.	
	July 27	18.5 per cent.	8.7 per cent.
	September 5	21.4 per cent.	5.5 per cent.
Station B.....	July 19	16.1 per cent.	11.7 per cent.

The light value of the Apinus flexilis formation was taken at a point where this formation overlapped the Picea Engelmanni–Abies lasiocarpa formation, on September 8 at 11:30 A. M. The observation was made in the general shade of the forest, not in the direct shade of a tree trunk. The value was 5:180.

(6) THE PSEUDOTSUGA MUCRONATA–PICEA ENGELMANNI FORMATION (*figs. 7, 8*)

This is the dominant formation of the cañons from 1800 to 2700^{m}. It mingles with the Pinus scopulorum and P. Murrayana formations

on the ridges and with the Populus angustifolia formation in the cañon bottoms. *Pseudotsuga mucronata* is more common than the other characteristic of the formation and is far more extensive in its habitat than the latter. Besides *Picea Engelmanni, P. Parryana* occurs in the formation, forming a straggling society along the bottom of the cañons from 2100^{m} to 2700^{m}. Both of these species are confined to the cool, moist cañon bottoms and the draws running into them. The Pseudotsugas, on the contrary, extend up on to the dry ridges to associate with the pines growing there. They come down the cañons to 1710^{m}, while the lowest limit of Picea is about 1950^{m}.

I have already mentioned the fact that Pseudotsuga, in the lower part of its range, is restricted to the north slopes.[11] A comparison of the physical conditions of the opposite slopes of Left Hand Cañon at an approximate altitude of 2100^{m} was made by me on September 20, 1905. Two stations were selected, one on the south side (north slope) of the cañon and the other on the north side (south slope). The former slope was well covered with aspens, the station being chosen in a little glade among them. The latter slope was sparsely forested with aspens and pines (*P. scopulorum*). Each station was about 9^{m} above the stream. The former I have designated as A and the latter as B. The following are my results, the observations being made September 20, 1905:

Temperatures

	−22.5^{cm}	−11.25^{cm}	0^{cm}	+7.5^{cm}	+0.9^{m}
Station A, 2:15 P. M.....	7°.5	9°.5	10°.5	20°.25	21°.7
Station B, 2:50 P. M.....	22°.5	19°	43°	28°.5	25°.5

Relative humidity

	7.5^{cm}	9^{dm}
Station A, 2:15 P. M..	32 per cent.	27 per cent.
Station B, 2:50 P. M..	25 per cent.	26 per cent.

*Water content**

	1^{m} depth	22.5^{cm} depth†
Station A.....	4.9 per cent.	11.3 per cent.
Station B.....	2.7 per cent.	3.3 per cent.

* The preceding evening was showery and rain probably fell at these stations.

† A few centimeters core was taken at each depth.

As the result of lumbering and fires, this formation has been extensively invaded by forms from adjoining open slopes, but typically

[11] In this connection see also JACK (*op. cit.*, p. 434, *pl. 12*); SHANTZ (*op. cit.*, pp. 34, 40); and RAMALEY (*op. cit.*, pp. 31 et seq.).

it is a closed formation admitting only a few shade plants. Where it overlaps the pine formations on the ridges, its secondary layer is the same as already described for them. In the cañon bottoms it is invading the Populus angustifolia–Salix Nuttallii formation, while it in turn is invaded by forms from the open cañon slopes. Where the tree growth is dense, however, it is practically exclusive of all

FIG. 10.—The Picea-Abies formation; approximate altitute 3300m; in the background is seen an extensive burned area.

forms except a few mosses and lichens and an occasional *Pyrola secunda* or *Arnica cordifolia*. The formation has been lumbered extensively, the Douglas fir being used to a considerable extent for rough bridge timbering and similar purposes.

For the physical characters of the habitat, reference may be made to the results recorded for the Pinus scopulorum formation, and for Station A in the Pinus Murrayana formation, since both of these sets of results are representative of the higher, drier parts of the Pseudot-

suga habitat. One other set of observations was made at the bottom of Boulder Cañon at 3:40 P.M. on August 29 at an approximate altitude of 2250m. Here *Picea Engelmanni* is common and the physical factors typical of the cool, moist portions of the habitat of this formation. The results obtained at this latter point are as follows:

Temperatures

−22.5cm	−11.25cm	0cm	+7.5cm	+0dm
11°.5	14°	17°	——	18°.7

Water content

11.25cm	22.5−11.25cm
135.7 per cent.	5.8 per cent.

(7) THE PICEA ENGELMANNI–ABIES LASIOCARPA FORMATION (*figs. 4, 10, 11*)

This formation occupies chiefly the cañons and to a lesser extent the ridges of the mountains from 2850m to timber-line, in the latter situation mingling with the Apinus formation. The two characteristic species are of comparatively equal abundance, although the firs are more numerous above 3000m and do not extend much below 2400m; while the spruces are more abundant below 3000m and pass down, as already noted, to 1950m.

Where the forest is virgin it forms a dense growth, excluding practically all forms except *Vaccinium microphyllum* and a few mosses and lichens. Along the wet stream banks through the forest, however, we find the brookside formation of the Hudsonian zone characterized by *Caltha leptosepala*, *Mertensia ciliata*, and *Senecio triangularis*, while occasional invaders from adjoining open slopes occur in the more open parts of the formation. Of these must be noted especially *Erigeron salsuginosus* and *Pedicularis racemosa*. It is doubtful whether the latter form is to be considered as an invader or not. It is more common in open timber than in clearings, but does not occur in the dense forest.

The results obtained from observations in the Apinus flexilis formation are representative of the drier part of the habitat of this formation. In addition to these results are those obtained at two other points within this formation. The first of these, which I shall designate as Station A, was near the head of a wooded cañon, and in

its lower part, at an approximate altitude of 3150m. The slope was gentle, the exposure southeast. The second point, which I shall designate as Station B, was in this same cañon at an approximate altitude of 3300m, on a steep south slope.

Temperatures

	Observations	−22.5cm	−11.25cm	0cm	+7.5cm	+0.9m
Station A* ..	June 20, 7 P. M.	——	——	4°6	8°7	8°7
	June 21, 6 A. M.	——	——	3°2	2°5	2°2
Station B....	September 22, 4 P. M.	7°25	8°25	14°75	——	——

* The observations at this station were made while many snowdrifts still lay in the forest.

Relative humidity

	Observations	+7.5cm	+0.9m
Station A.....	June 20, 7 P. M.	40 per cent.	40 per cent.
	June 21, 6 A. M.	100 per cent.	96 per cent.

Water content

	Observations	11.25cm	22.5−11.25cm
Station A.....	June 20, 7 P. M.	227 per cent.	—— per cent.
Station B.....	September 22, 4 P. M.	20.9 per cent.	20.9 per cent.

Light value

For light value, refer to Apinus formation.

(8) THE ASPEN SOCIETY (*fig. 9*)

I have already stated my reasons for not considering the groves of aspens as a distinct formation. They have an individuality as a society, however, among the other forest formations which entitles them to separate consideration at this point.

This society occurs within the limits of the other formations. It usually occurs as a distinct society, but occasionally loses its individuality, mingling intimately with the trees of the other forests. It is distributed throughout the mountains from 1800m to 3150m, being confined in the lower part of its range to the north slopes, but in the higher mountains being distributed indifferently over both north and south slopes. It may occur either as a scattered grove of trees, exercising but little if any control upon the lower layers of the vegetation; or it may form a forest with the trees growing within a few feet of each other, in which case it does exercise a decided control upon the lower layers.

The physical conditions in such a forest are intermediate between those in the dense spruce and fir timber of the cañon bottoms and

the exposed mountain slopes. The height of the trees and density of the foliage is not such as to produce more than a moderate amount of shade, so that the under layer is not composed exclusively of dense shade-loving species, while the amount of moisture retained by the soil is sufficient to support an abundant growth of plants. The under layer is mixed and for the most part open. Some of the more frequent members are *Artemisia tridentata*, *Arctostaphylos uva-ursi*, *Achillea lanulosa*, *Poa triflora*, *Antennaria parvifolia*, *Poa pratensis*, *Aquilegia coerulea*, and *Castilleja acuminata*.

A series of three observations of the physical characters of the habitat of this formation, taken at a point at 2490^{m} altitude approximately, in a little hollow where the general slope was southwest and very gradual, gave the following results,[12] the observations being made July 5, 6:10 P. M.; 25, 4:05 P. M.; August 28, 5:45 P. M.

Temperatures

	−22.5^{cm}	−11.25^{cm}	0^{cm}	7.5^{cm}	9^{dm}
Minima	14°5*	12°	11°2	11°	11°5
Maxima	14°5*	16°	19°†	17°5	18°25

Relative humidity

	7.5^{cm}	9^{dm}
Minima	68 per cent.	55 per cent.
Maxima	89 per cent.	71 per cent.

Water content

Observations	11.25^{cm}	22.5−11.25^{cm}
July 5	17.3 per cent.	——
July 25	21.1 per cent.	7.9 per cent.
Aug. 28	20.9 per cent.	9.1 per cent.

Light value

August 27, 10 A. M. ..... =5:90

* One observation only, August 28.

† Four observations, this recorded on July 14.

CLEMENTS,[13] recognizes the following forest formations in the Pike's Peak region of Colorado: Pinus edulis–Juniperus (monosperma); Pinus ponderosa–flexilis; Populus tremuloides; Picea Engelmanni and Parryana–Pseudotsuga (mucronata); Picea Engelmanni–Pinus (aristata). The first of these is not represented in Boulder County. My reasons for recognizing the Pinus scopulorum,

[12] See also the results obtained at Station A on September 20.

[13] CLEMENTS, F. E., Formation and succession herbaria. Univ. Nebr. Studies 4:329–355.

Apinus flexilis, and Pseudotsuga formations as distinct, and for degrading the Populus tremuloides formation to the rank of a society, have been given in detail in the discussion of these formations. *Pinus aristata* is a southern form not occurring in this region so far as I know.

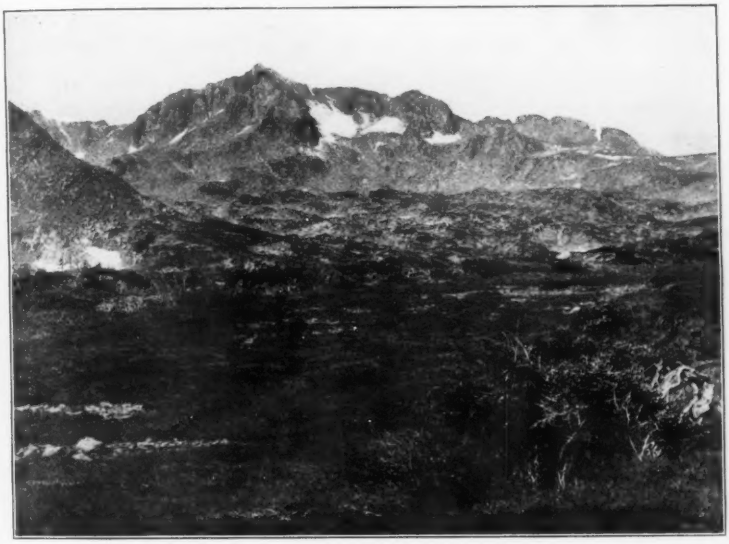


FIG. 11.—Timber-line on Mt. Arapahoe, south slope; approximate altitude 3450m; to the right is a small clump of spruce and fir.

Invasion and succession

The soil of the mountain sides is the result of disintegration of the talus slopes with which they are covered. It is a loose gravel composed of particles of rotten granite, which is very readily eroded and forms an unstable foothold for plants. It is continually working its way downward into the cañons.

I have been unable to determine any sharply defined successional stages within any of the forest formations. The first invaders of a new or denuded soil are determined primarily by proximity, secondarily by mobility. On rough talus slopes, where there has been as

yet but little disintegration, the principal forms present are the lichens, but even here occasional shrubs and grasses may be found growing in crevices where a little soil has collected. On loose gravel slopes denuded by erosion, herbs, shrubs, and even trees from neighboring formations, may pass in indiscriminately. Along railroad cuts and embankments and in new soils generally, which are close to highways or other paths of ruderal migration, those forms are among the first invaders, but they are not exclusively the first to enter. Associated with them are forms from the surrounding formations, and these may be either herbs or shrubs, while in some instances trees are the first invaders of a new soil. As an instance of the latter we have the invasion of sand flats on Boulder Creek by *Populus occidentalis*.

All of the forest formations of the higher mountains have been extensively denuded by fire (*figs. 3, 10*). The Pinus scopulorum formation has not recently been burned extensively, due doubtless to the fact that the pines form such a scattered growth that it is difficult for fires to spread to any extent among them. While the aspens play a large part in the reforestation of these burned areas, owing to the mobility of their seeds and the readiness with which they reproduce from roots left uninjured in the burned area, their share in reforestation is not exclusive. Thus any other of the forest trees may reforest a denuded area without the intervention of any aspen stage in the succession, while pines and aspens may reforest a denuded area simultaneously.

In the numerous meadows of glacial origin in the higher mountains, there is proceeding a gradual invasion of the meadows by the Picea-Abies forest adjoining them, the latter representing the final stage in a succession initiated by mosses, sedges, and grasses; these in turn to be replaced by beeches and willows, and these latter finally to make way for the forest. These stages, however, are not sharply defined. The forest may succeed the sedges and grasses directly, without the intervention of willows and beeches, or the latter may succeed the grasses and sedges simultaneously with the forest.

The life-zones of the mountains in Boulder County may be outlined as follows, based upon the forests of the region: *Alpine zone*, characterized by absence of trees, above 3300 to 3450^{m}; *Hudsonian zone*, characterized by *Apinus flexilis* and *Abies lasiocarpa*, 2850 to 3450^{m};

Canadian zone, characterized by *Pinus Murrayana*, 2400 to 2850^{m}; *Transition zone*, characterized by *Pinus scopulorum*, 1650 to 2400^{m}.

While physical factors are so closely interrelated that it is very difficult to separate them in determining what factors exercise the greatest influence in limiting the formations, we may at least limit these factors to two in answering the question "Why are zones present in mountain forests?" The factors of light and humidity may be rejected at once, since their variation at different altitudes is practically

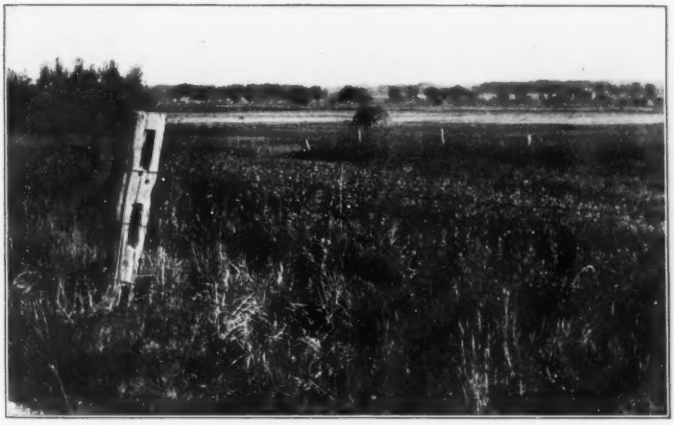


FIG. 12.—The Populus occidentalis formation in the valley of Boulder Creek, six miles east of Boulder; approximate altitude 1590^{m}.

negligible. The obvious answer is that mountain zonation is due entirely to temperature. We have already seen that the difference in temperature between timber-line and the base of the mountain is very marked and the same is true, even to a greater extent, of the length of the growing-season. That water content may play as great if not a greater rôle than temperature, however, is at least possible. I have already noted the fact that the rainfall in the high mountains is about 25^{cm} more annually than on the lower slopes.

The part played, moreover, by the development of the formations and their relation to the glacial history of the country may be very

considerable. At present I have not sufficient data to enable me to discuss this question fully.

In closing this paper, I wish to express my appreciation of the kindly interest taken in my work, and assistance given me by Drs. C. E. BESSEY and F. E. CLEMENTS, of the University of Nebraska, and by Dr. FRANCIS RAMALEY, of the University of Colorado. For identification of my collection I am indebted to the New York Botanical Garden, Professor AVEN NELSON, Laramie, Wyoming, and Mr. A. S. HITCHCOCK, of the United States Department of Agriculture.

UNIVERSITY OF NORTH DAKOTA

FERTILIZATION IN CYPRIPEDIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 103

LULA PACE

(WITH PLATES XXIV–XXVII AND ONE FIGURE)

The orchids have attracted much attention on account of their striking habits and especially because of their remarkable adaptations to insect pollination, but the record of morphological investigation is a very scanty one. Morphologists have doubtless regarded them as highly specialized forms, whose interest probably lies within themselves rather than in any connection with the larger problems at present attracting attention. In the stages of development extending from the archesporium of the ovule to fertilization, STRASBURGER'S account (**43**) of *Orchis pallens*, in 1878, indicated that the familiar angiosperm stages were present in the family. Later, the same investigator (**44**) states that no parietal cell is cut off in *Gymnadenia conopsea;* and GOEBEL (**22**) makes a similar statement for *Orchis pallens*, probably based upon STRASBURGER'S original account of this species; but DUMÉE and MALINVAUD (**19**) report several genera with parietal cells. Recently NAWASCHIN (**35**) and STRASBURGER (**45**) have discussed triple fusion in the orchids and its relation to endosperm development, the former claiming that in tropical forms the nuclei remain in contact but do not fuse, the latter stating that fusion occurs in the forms he had investigated. In connection with the development of the embryo, especially in reference to certain remarkable suspensors of the group, there is a considerable body of literature, but it lies beyond the scope of this paper.

The greater part of the material for the present investigation was collected in the vicinity of Chicago in the summer of 1906, small collections having been made also in 1896 and 1898. The collections of 1906 were made June 17, July 4, 11, 17, and 27. *Cypripedium spectabile* and *C. parviflorum* furnished the greater part of the material, but *C. pubescens* and *C. candidum* were examined also in a few stages. The youngest material collected was from flowers just

opening, and later stages were collected from time to time until the seeds were almost mature.

MEGASPORE

As is well known, the ovary of orchids contains a great number of small ovules arranged in three double rows. The ovules are very slow in developing, but the archesporial cell is differentiated in the bud. No parietal cell is cut off, the archesporium functioning as the spore mother cell. The young ovule lengthens rapidly and a row of several cells is formed below the archesporium; these cells were often seen in mitosis, but the archesporium was never found dividing until the mother-cell stage. In flowers just opening the spirem of the mother cell is formed, and the synapsis stage is usually reached by the time the flower is in full bloom (*fig. 1*). While the division of the mother cell appears to be of rather long duration in most plants, it seems to be unusually prolonged in orchids as compared with other herbaceous plants. Certain cultivated orchids examined suggest the probability of no further development of the ovule unless pollination takes place. The cells of the ovule are all relatively large, with large nuclei, but the mother cell is quite striking because of its size. At this stage the whole ovule, which is always very small, is growing rapidly, the region of the integuments being especially active. The division of the mother cell takes place in the usual way (*figs. 1, 15, 16*).

Certain details of this division are particularly well shown in my material. After the integuments are started, the spirem begins to thicken, the chromomeres are very distinct, and the thread is quite long, so that it is hardly possible to do more than suggest its appearance in a drawing (*fig. 2*). A nucleus like that in *fig. 3*, in which only a few threads are drawn, shows them beginning to be paired; a little later stage is shown in *fig. 4*, where the threads lie closer together and pairing is more evident, the whole spirem being in this condition. In this stage the chromomeres were not so distinct, but it was evident that the threads were not entirely homogeneous. When the threads have approached each other until the chromomeres almost touch, or even seem to be in contact, the synaptic knot begins to form (*fig. 5*), usually around or close to the nucleolus, which often shows vacuoles at this time. As the threads are crowded more and more into the

knot, often several of them seem to be attached to the nuclear membrane (*fig. 6*); this was seen several times, so that it is probably the usual condition. The synaptic knot is at one side of the nucleus and gradually becomes a compact mass (*fig. 7*). Even when it is most compact, the constituent threads are apparently distinct, as is suggested in the figure by the rough edges of the knot and by the very evident lines across it. Hundreds of nuclei in this stage were examined and this seems to be the usual condition.

Upon coming out of synapsis, the threads are no longer in distinct pairs, but in many instances the double nature could be detected for short distances, and occasionally throughout much of the spirem. The threads gradually resume their position near the nuclear membrane (*figs. 8, 9*), and about this time the cytoplasm becomes arranged in lines which radiate from several centers (*figs. 8, 11*), which are evidently the first indications of the multipolar spindle. The chromomeres become less and less distinct, so that with the thick spirem an almost perfect homogeneity seems to exist (*fig. 9*); but even in this stage the double nature of the spirem is often evident, especially when cut ends are examined. There are eleven chromosomes at this reduction division (*figs. 12, 13*), but it was not possible to determine just how the splitting takes place—whether transversely or longitudinally. *Fig. 10* is at the right stage, but whether these pieces are to be regarded as having about completed the longitudinal splitting, or as the one long curved and twisted chromosome which will be cut transversely, could not be determined from my material. *Fig. 15* shows a typical spindle for the division of the mother cell. A cell in the wall of the ovule gave the expected count of twenty-two chromosomes for the sporophyte; these were scattered somewhat in the drawing (*fig. 14*).

When first formed, the daughter cells are alike in form and size (*fig. 16*); but very soon the inner cell shows that it is developing faster than the outer (*fig. 17*), which also begins to show signs of disintegration. This difference becomes more and more pronounced in the metaphase (*fig. 19*) and telophase (*fig. 20*) of the favored cell. Early indications of the spindle suggest the usual bipolar form (*fig. 18*), and longitudinal splitting of the chromosomes is shown in *fig. 19*, so that there is nothing unusual in this division of the daughter

cell (or cells) up to the telophase stage. There is no evidence of a wall forming between the two nuclei either in the telophase stage or later; and the two nuclei are thus left free in the cytoplasm. This stage was seen repeatedly, and never was there a wall separating the megaspores formed by the second division. *Figs. 20, 21, 23, 24* represent conditions common in the material studied, which was collected July 11, when the flowers had withered. This is the condition in most flowers when one looks for fertilization stages; but here the megaspores are just forming in many of the ovules, although in an occasional one there was some evidence of fertilization. The figures give a rather complete series of the stages that would be expected to show indications of wall formation; but there is no suggestion of an ephemeral wall even, as might be expected in case of its relatively recent elimination. *Fig. 22* shows two daughter cells in which the nucleus of the micropylar one is developing, but this was the only case of the kind seen.

EMBRYO SAC

Immediately after the division of the inner daughter nucleus, forming two megaspore nuclei with no wall separating them, these two nuclei organize the embryo sac (*fig. 23*), which increases rapidly in size and becomes very vacuolate. The two megaspore nuclei form spirems (*fig. 24*) which thicken, and the usual mitotic division follows (*fig. 25*). The spindles for this division, resulting in a four-nucleate sac, are small and apparently at right angles to one another. No evidence of another division was found, although at least three hundred slides with hundreds of ovules upon each were examined for this particular stage. When the sac is ready for fertilization, four nuclei are present, so that if other nuclei are formed they are very ephemeral. The micropylar daughter cell resulting from the division of the megaspore mother cell may still be distinguished, though it is evidently fast disintegrating (*figs. 23, 24, 25*). The four nuclei of the sac are usually of the same size (*fig. 26*), but in one instance the two micropylar ones were larger than the others (*fig. 27*). Probably *fig. 28* gives the explanation; in this sac the two megaspore nuclei are not dividing simultaneously, the antipodal one being in late prophase, while the micropylar one has reached the late telophase

and the two new nuclei are being organized. Not only has the embryo sac increased enormously in size, but the whole ovule is very active. The integuments have grown very rapidly, having lengthened until they reach far beyond the nucellus.

The usual egg apparatus, with its two synergids and egg, each with very distinct cytoplasm and *Hautschicht*, is organized in the micropylar end of the sac, the other nucleus being left in the center or toward the antipodal end (*figs. 29, 30*).

A few peculiar or "abnormal" forms were found. *Fig. 31* shows what appears to be two mother cells, which is suggested by the unusual development of that region of the ovule compared with that of the integuments and the remainder of the ovule; but the best evidence is in the chromosomes, which in both cells appear to be of the heterotypic form. In another orchid, in several cases, two mother cells (in synapsis) were seen in a single ovule. Usually the spindle in the division of the mother cell is parallel with the axis of the ovule; but *fig. 32* shows one at right angles to the usual position; only two of these spindles were seen, and they were near each other in the same ovary. No arrangement of megaspores seen could be related to this position of the spindle. Several examples of the division of both daughter cells were found (*fig. 33*). It is probable that in this case only one embryo sac is formed, for even in the very early spirem stage the two chalazal megaspores are developing at the expense of the others, or at least more rapidly than the two micropylar ones (*fig. 34*). The width of the ovule in *fig. 35* suggests the possibility of a transverse spindle, but it was evidently transverse in the second division, as suggested by the lines of protoplasm and by the position of the nuclei. These "abnormalities" are all rare in my material, not more than a dozen such cases appearing among thousands of the usual forms.

FERTILIZATION

The immense number of ovules suggested the possibility of parthenogenesis, or of failure to develop an embryo at all. The latter view is favored by the well-known difficulty in germinating orchid seeds, but the material studied gave no indication of either condition. All ovules of the right age had embryos, and in almost all of them evidences of the pollen tube were more or less distinct, traces of it

often being detected in the space between the wall of the ovary and the micropyle; and in most cases traces could be seen in the micropyle and continuing into the embryo sac (*figs. 43, 49*).

In the pollen grain the division into tube end generative cells takes place before shedding. In this division a wall forms in all cases examined, but it soon disappears. In one anther over one hundred late anaphases and early telophases were counted in which the wall was formed, and only about a dozen late telophases were without a wall. As these showed no traces of the spindle, the probability is that the wall was formed here as in the others, but had disappeared. The generative nucleus has a mass of cytoplasm about it that differs markedly in its staining reaction from that of the tube nucleus. The gametophyte number of chromosomes (eleven) was easily counted here. *Figs. 36–41* represent a series in this division. *Fig. 39* shows the wall forming in the telophase, while *fig. 40* shows it completed. The latter figure is also interesting in showing a chromosome left out of one of the nuclei at its organization.

The division of the generative nucleus was not seen; but as pollen from the bud to the time of shedding was studied, it must take place after pollination. When the pollen tube is passing from the ovary wall to the micropyle, the division has already taken place (*fig. 45*).

Only one attempt at pollination was made. Two flowers with stems about 25^{cm} long were brought into the laboratory, placed in water, and the whole put under a bell jar with some ventilation to keep them in as nearly normal condition as possible. Each was pollinated from the other. Four days later one of them was fixed, being apparently in good condition; but the other was dead six days after pollination. When the first was sectioned and stained, the ovules were found to have gone to pieces. The pollination was made in the hope of getting some idea of the development of the ovule in relation to the time of pollination. The stigma was sectioned and showed that the pollen grains had practically all developed tubes, many of them being traced into the conductive tissue, in some cases for some distance, and the grains were almost all empty. If the development of the tube was delayed, a condition like that in *fig. 41* was found, in which the tube is just forming and the generative nucleus is beginning to show signs of activity. Soon a complete

spirem is formed, and tubes less than the length of the pollen grain have the three nuclei in them; so that the generative nucleus probably divides into the male nuclei as the tube develops.

It will be remembered that the embryo sac ready for fertilization contains only four nuclei—the egg apparatus in the usual position, and the remaining nucleus near the center of the sac or toward the antipodal end (*figs. 29, 30*). As the pollen tube penetrates the sac, one of the synergids may be in front of it and a little lower than the other, as if it were being pushed from its usual position by the inrush of the contents of the tube, or moving for some other reason toward the antipodal end of the sac (*fig. 44*). The egg nucleus may be already in the spirem stage. The pollen tube here shows the tube nucleus in advance, with the two male nuclei elongated and near it. A stage just later than this shows two nuclei below the egg, and from the lines of cytoplasm one seems to be the synergid which has moved to that position (*fig. 42*). The two male nuclei are still somewhat elongated and are in advance of the tube nucleus. *Fig. 43* shows the polar nucleus and the synergid near the antipodal end of the sac, and the two male nuclei still elongated. The primary endosperm nucleus is formed in this case by the fusion of a male cell, the solitary polar nucleus, and the migrating synergid. In this fusion, as well as in the fertilization of the egg, the fusing nuclei often come into contact in the resting condition (*fig. 45*), the figure showing the male nucleus in contact with the egg still curved and elongated. Many views of this stage might be given with slight variation in the position of the nuclei; and while fusion in the resting condition was apparently the more common in my material, it was not at all uncommon to find spirems already well formed and in different stages of development.

The pollen tube was often traced from the ovary wall through the micropyle into the embryo sac. The male nuclei are usually elongated and sometimes in advance of the tube nucleus, but the tube nucleus usually precedes them (*fig. 46*). In no case does the pollen tube pass directly to the micropyle, but bends in various directions. This may be due to the attraction of other ovules, several of which will be almost as near as the one entered. It may be that after leaving the ovary wall the tube simply wanders in this space until it comes within the influence of the ovule it enters.

One sac indicated the possibility that the synergid may fail to unite in the triple fusion. *Fig. 47* is unusually interesting. Some of the nuclei show the tendency to become amoeboid, but the interest is due especially to the condition of the nuclei, all of those that take part in double fertilization having reached the spirem stage not only before fusion, but even before contact. The spirem is well formed in every nucleus, and shortened almost enough to segment into chromosomes. It would seem in this case that if fusion does take place, there could be no possibility of a fusion of the chromatin, which would certainly divide into chromosomes from each spirem as it is now formed. Well-formed spirems in different stages of development are common; in *fig. 48* the male and female nuclei have formed thick spirems which are evidently distinct, and while those of the triple nucleus are just as distinct, they are much younger. In the same figure an unusual development of the synergid, or possibly of the tube nucleus, is shown; but as no further indication of division was ever found, there is probably no significance to be attached to it. *Fig. 49* shows a pollen tube from its entrance into the micropyle to its ending in the sac, the male nuclei being not only elongated but curved. In a few instances there is some distance between the two male nuclei (*fig. 50*), but this seems to be rather uncommon. The very sharp bend in the tube shown in the last figure suggests some special attraction felt just at this point, directing the tube into the micropyle.

ENDOSPERM

The fertilized egg may divide before the primary endosperm nucleus (*figs. 51, 52*) and during this division the latter may be in the spirem stage (*fig. 51*), or resting, or with the spirem just forming; and in one instance the division of the egg was taking place before the second male nucleus had left the pollen tube. The endosperm nucleus, however, may divide first, *fig. 53* showing it in late prophase while the egg and male nucleus are barely in contact and the spirem is just beginning to be formed in each.

With the nuclei of both fusions in the spirem stage the endosperm nucleus may be farther advanced than the egg, one preparation showing its threads very distinct and much thicker than those of the

egg. *Fig. 54* shows a two-celled embryo and the primary endosperm nucleus in late prophase. At the three- or four-celled stage of the embryo, the endosperm nucleus shows a spindle forming (*fig. 55*), which is almost complete and is very broad; the chromosomes (approximately thirty-three) are probably in metaphase. On the other hand, the primary endosperm nucleus may reach the anaphase before the fusion of the male and female nuclei, as one of my sections shows, the male nucleus not having left the pollen tube, and both it and the egg nucleus with spirems forming.

The telophase of the endosperm spindle shows a wall (*fig. 56*), but it is probably ephemeral, as none was seen either in two- or four-nucleate endosperm. The endosperm nuclei are relatively large, as would be expected from the large amount of chromatin used in their formation (*figs. 57, 58*), one in *fig. 57* measuring 17×23 μ. For this reason they are not likely to be confused with other nuclei of the sac. The two-nucleate stage of the endosperm may be reached at any stage of the embryo between two and twenty or more cells. The figures for the second division of the endosperm were not seen, but the four-nucleate stage was found in a few sacs (*fig. 58*). From the appearance of these nuclei it is altogether probable that another division may take place, for they are apparently beginning the formation of the spirem for the next division, and are large, vigorous-looking nuclei.

While the presence of endosperm nuclei is quite common, it is not difficult to select a series that would indicate the possibility of their failure. An embryo of several cells with the primary endosperm nucleus still in the resting condition is rare (*fig. 59*); but we need not conclude that division may not take place later than this, for with a still older embryo (*fig. 60*) the endosperm nuclei have begun to form spirems, although there is no evidence of fusion further than the contact. In *fig. 61* one of the nuclei, probably the male nucleus, has been delayed in reaching the other two; yet some suggestion of the spirem is evident in all three. *Fig. 62* shows a sac which is almost filled by the embryo, and at the base are three nuclei which are probably the constituents of the triple fusion which has not taken place; it is barely possible that they are endosperm nuclei, but there is no evidence of a fourth nucleus. If these are not endosperm nuclei,

it is evident that in this case none will be formed, for all of them show signs of disintegration.

EMBRYO

The embryo is very simple. As stated above, the fertilized egg may divide before the primary endosperm nucleus, which seems to be the more common behavior in my material; or the primary endosperm nucleus may divide first (*figs. 51–55*). An inconspicuous suspensor of one or two cells is formed, but no other differentiation of regions could be made out in the younger stages (*figs. 55, 62*). The number of chromosomes in the segmentation of the egg seemed to be twenty-two (*figs. 51, 52*), and this number was counted several times in various parts of the ovule (*fig. 14*).

DISCUSSION

It is unfortunate that there is no definite name for the two cells resulting from the division of the megaspore mother cell. "Daughter cells" has been used in this paper to designate them. It has been customary to call the cell that develops the embryo sac a megaspore, and this is correct in all cases when the sac is organized from the chalazal cell in the "row of three" or from one of the cells in the "row of four." But if the name is applied to one of the "daughter cells" there is confusion, for in this case the reduction process is not complete.

MEGASPORE.—In angiosperms two types of embryo sac have been recognized: (1) the more common type, in which the mother cell gives rise to four megaspores, one of which develops the sac; (2) the Lilium type, in which the mother cell, "functioning as a megaspore," forms the sac directly. In the former case, the occasional "row of three" does not change the situation, for the functioning megaspore is derived from the mother cell by two successive divisions (COULTER and CHAMBERLAIN **16**).

The production of only two "megaspores" ("daughter cells") by the mother cell has been reported for a few plants that usually form megaspores in the normal way. SCHNIEWIND-THIES (**40**) reports two or four in Galtonia; GUIGNARD (**25**) two in Agraphis, Ornithogalum, and Commelina; MOTTIER (**31**) two in Arisaema (in one instance with no wall between them, which would present the

Lilium condition); CAMPBELL (**7**) two or three in Dieffenbachia; and JUEL (**29**) two in Taraxacum. The very few cases reported show the rarity of this condition among the angiosperms investigated. Four of the five families represented in this enumeration, to which the Orchidaceae are now added, are all monocotyledons; and this fact, taken together with the still greater reduction in the Lilium type, is in harmony with the theory that monocotyledons are a specialized offshoot from dicotyledons, as held by JEFFREY (**28**), QUÉVA (**37**), Miss SARGANT (**38**), and others.

However, SCHNIEWIND-THIES (**40**) has shown that in Lilium the heterotypic and homotypic divisions take place within the embryo sac; that is, there is no permanent wall formed in either of the divisions from mother cell to the four megaspore nuclei. It follows, therefore, that all four megaspore nuclei take part in forming such an embryo sac. In Cypripedium, on the other hand, a wall accompanies the first division of the mother cell, but no wall is formed in connection with the second division. In this case, therefore, two megaspore nuclei enter into the formation of the embryo sac, instead of four as in Lilium, or one as in most angiosperms. It is interesting to note here that if the usual megaspore walls were formed in Lilium and in Cypripedium, each sac would contain two nuclei—the egg and its sister, which is the polar that usually unites with the antipodal polar to form the primary endosperm nucleus.

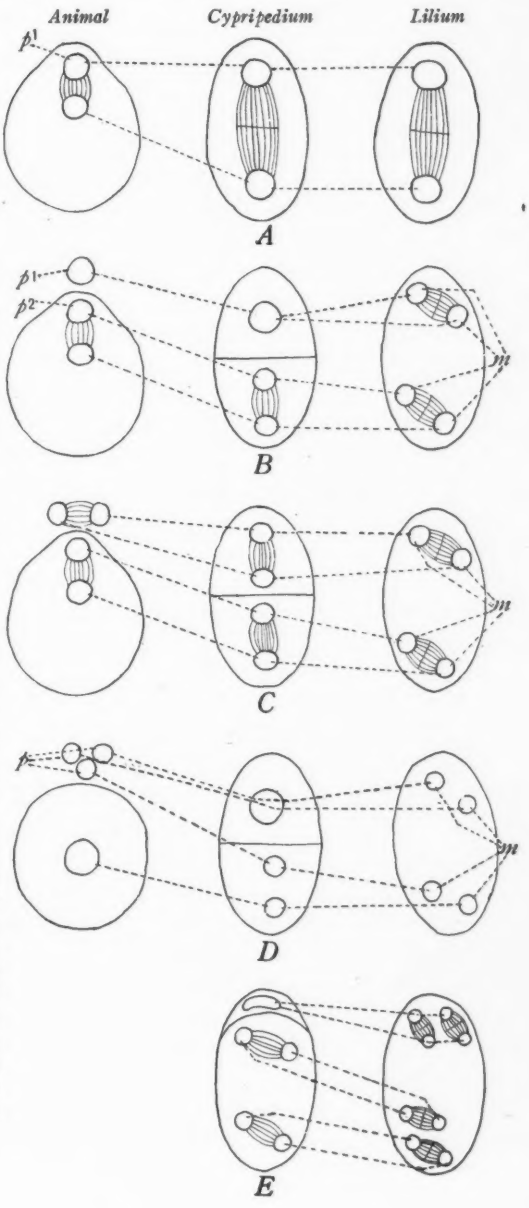
EMBRYO SAC.—An embryo sac with only four nuclei has not been reported before, but there is just the same number of divisions between the mother cell and the egg in this case as in Lilium. After all, the essential feature in the history of the egg is the distribution of the chromosomes in the reduction divisions. It is possible that the use of more than one megaspore in organizing the sac holds some necessary relation to "double fertilization," for in both Lilium and Cypripedium, if walls appeared in the usual way so that only one megaspore was used in forming the sac, and there were no additional divisions between mother cell and egg, there would be only two nuclei in the sac, and "double fertilization," at least "triple fusion," would be impossible.

It is interesting in this connection to compare this series with that in the animal egg. There the primary oocyte (mother cell)

divides and throws off a polar body, and forms the secondary oocyte. The polar body may divide; the secondary oocyte divides, forming another polar body and the mature egg (megaspore) (see BOVERI **6** and WILSON **47**). The two divisions are of the heterotypic and homotypic types found in plants in the formation of megaspores. In Cypripedium, if the last division in the embryo sac were omitted, there would be the same number of divisions in the formation of the egg as in the animal. If the wall were omitted between the daughter nuclei at the division of the mother cell, as in Lilium, and the last division were omitted, the sac would have four nuclei as now; and this would be true of Lilium if the last division did not take place. This situation was discussed by CHAMBERLAIN (**11, 12**) in connection with the usual eight-nucleate sac, and also in relation to the probable four-nucleate sac of Cypripedium.

The situation may be made more clear by means of diagrams. *Fig. A* represents the primary oocyte dividing in the usual way and the mother-cell division in Cypripedium and in Lilium; in all cases this is the heterotypic division. *Fig. B* represents the next division if the first polar body fails to divide, and if the micropylar nucleus fails as in Cypripedium. *Fig. C* represents the same stage as *fig. B*, but the first polar body and the micropylar cell in Cypripedium divide; this is the homotypic division. *Fig. D* represents the division indicated in *fig. C* completed, with the typical arrangement of nuclei in all three forms. This completes the animal series; but in Cypripedium and in Lilium there is another division, which is represented in *fig. E*. It is evident that in these forms there is even greater reduction in the number of divisions than in the male gametophyte if the mother cell be taken as the beginning of the gametophyte generation, as is done by COULTER and CHAMBERLAIN (**17**); for there the male nucleus represents two divisions beyond the microspore, while in Cypripedium and Lilium the egg is removed by only one division from the megaspore nucleus.

WALL IN POLLEN GRAIN.—The ephemeral wall in the pollen grain between the tube and generative nuclei is not difficult to explain according to present homologies. It has been reported in a few plants, as Neottia (GUIGNARD **26**), Sarcodes (OLIVER **36**), Naias and Sparganium (CAMPBELL **8, 9**), Populus and Lilium (CHAMBERLAIN



Successive stages in maturation of animal egg, and in development of megaspores in Cypripedium and in Lilium. *A*, the division of the primary oocyte to form the first polar body (p^1) and the secondary oocyte; and the division of the mother cell in Cypripedium and in Lilium—all heterotypic divisions. *B*, the division of the secondary oocyte to form the second polar body (p^2) and the egg; and the second division in Cypripedium and in Lilium, giving the megaspores (*m*)—the homotypic division in all. *C*, the same stage as the preceding, but the first polar body of the animal and the micropylar nucleus of Cypripedium dividing. *D*, the egg and the three polar bodies (*p*) of the animal, and the megaspores (*m*) of Cypripedium and of Lilium. *E*, not in the animal series; the division that gives the egg in Cypripedium and in Lilium.

13, 14), Sagittaria (SCHAFFNER 39), Convallaria (WIEGAND 46), Asclepias (FRYE 21), and Hamamelis (SHOEMAKER 41). If the tube cell represents the wall cells of the antheridium, this wall is a relict of the time when there was a complete separation between spermatogenous and wall tissue (COULTER and CHAMBERLAIN 18). This difference was shown not only by separating walls but by reaction to stains; and the latter difference still remains in the pollen grain after the wall disappears.

DOUBLE FERTILIZATION.—In looking over my material it seems strange that double fertilization was first reported less than a decade ago, when NAWASCHIN (33, 34) made his announcement. In my material double fertilization was observed in hundreds of instances; in fact there would be some difficulty in finding fertilization without some suggestion of triple fusion; it was as evident in every respect as the fertilization of the egg. However, it was stated above that in some cases it may fail to take place; and it would not seem unlikely that in some orchids triple fusion always occurs and in others it may be rare or omitted altogether, as indicated by STRASBURGER and NAWASCHIN. NAWASCHIN thought that in the failure of triple fusion he had found the explanation of the lack of endosperm in orchids, but it is evident that the little or no endosperm of this family must be referred to other causes. It may be accurate enough for taxonomic purposes to say "no endosperm" in the orchids, as in a recent manual (42), but it is not an exact statement.

DISTINCT PATERNAL AND MATERNAL CHROMOSOMES.—Some important evidence on this much-discussed question was obtained. This condition was first reported in plants by KRUCH (30), who worked with the liverwort, *Riella Clausonis;* but at that time (1891) it attracted little attention and seems to have been entirely overlooked by later workers. KRUCH showed the sperm entering the egg and segmenting in the upper part of the cytoplasm, while the chromatin of the egg-nucleus segments near the center, each showing eight chromosomes, and the nuclei were not even in contact. BLACKMAN (2), working with *Pinus sylvestris,* figured two groups of chromosomes in the first division of the fertilized egg and says: "there can be little doubt that these bodies are really the chromosomes of the two (male and female) nuclei." In his summary he makes the positive statement that they

are the chromosomes of the male and female nuclei. CHAMBERLAIN (**15**) in *Pinus Laricio* finds that "the chromatin appears as two distinct masses in the spirem stage. Perhaps segmentation of the two spirems occurs while they are still separate." MURRILL (**32**), working with *Tsuga canadensis*, says: "The chromatin of each (sperm and egg) nucleus collects in the form of a thick knotted thread near the center of the separating partition, and the two masses remain distinct until the spirem band begins to segment." Miss FERGUSON (**20**), using Pinus, finds "two groups distinct at time of segmentation of spirem and can still be made out during early development of chromosomes; but cannot be when they are being oriented on the nuclear plate." Recently HARPER and BLACKMAN have shown interesting features in some of the fungi that seem to be related to this independence of chromosomes. HARPER (**27**) has shown in Phyllactinia that "the material of each chromosome is in permanent connection with the central body throughout the stages of nuclear fusion and the resting condition, as well as in mitosis." BLACKMAN (**1**) says that rusts which have the aecidial stage have two nuclei in all cells from the aecidiospore to the teleutospore. The two nuclei fuse in the teleutospore and from there to the formation of the aecidiospores the cells are uninucleate. More recently GRÉGOIRE (**23**), working with roots of Allium, claims that the chromosomes do not unite to form a continuous spirem in the telophase, but always remain distinct bodies.

In my material, as shown above, it is quite common to find both the fertilized egg nucleus and the triple-fusion nucleus with distinct spirems in all the nuclei entering into the fusion (*figs. 42, 43, 44, 47, 48, 51, 53*). In one instance the spirems were all well advanced, so that the threads were quite broad, before contact of the nuclei (*fig. 47*). Spirems as far along as these will evidently be cut into chromosomes without fusing at all. If spirems are often formed separately, it would seem probable that when the nuclei fuse in the resting stage two separate spirems may still be present. Anyone who has tried to trace a spirem will at once recognize how difficult it would be to trace two of these long threads in the same nucleus; and as no one expected to find two, only one was seen until two were found distinctly separated. If there may be two spirems in the first

division of the sporophyte, why might it not be true of all the mitoses in the sporophyte generation? This would make half of the chromosomes paternal and half maternal in every sporophyte cell. Thus in the mother cell two spirems would be formed as usual, but here they would pair and fuse more or less completely in synapsis. If there are two phenomena in fertilization—stimulus to growth and the mingling of ancestral qualities—only the first would be felt in the sporophyte. The mother cell would give the opportunity for the second during the fusing of the pairs of threads.

The chromosomes of the fusing nuclei are often arranged in groups, and while these may not be definite enough to be positive evidence for distinct chromatin if taken by themselves, they are not only very suggestive but appear as distinct as the position of the nuclei in the spirem stage would lead one to expect (*figs. 51, 54*). In a form in which the paternal and maternal chromosomes differ, proof could be obtained; but even in Cypripedium, in such groups as those shown in *figs. 51–54*, the chromosomes are evidently of separate spirems. This seems very clear when these figures are studied in connection with those showing the spirems (*figs. 42, 43, 44, 47, 48, 51, 53*). The groups are just about as distinct as would be expected, for the nuclei usually overlap slightly in the spirem stage.

SYNAPSIS.—BERGHS (**3, 4, 5**), GREGORY (**24**), CARDIFF (**10**), and others have recently discussed synapsis and the stages leading up to and following this condition. It seems to be clearly established that in the forms studied by these authors there is a gradual pairing of the threads, beginning with the first suggestion of synapsis. The two threads are apparently united into a single thread by the time the nucleus comes out of synapsis. During synapsis itself and in early stages of the recovery from this condition some traces of the double nature of the thread are often seen, and the heterotypic chromosome is formed from this doubled thread. These stages were well shown in my material (*figs. 2–11*). BERGHS sees in this a device for reducing the number of chromosomes, but it may also furnish the opportunity for mixing of parts, or transfer of substance, or influence from the paternal and maternal chromosomes that have remained distinct throughout the sporophyte stage. CARDIFF (**10**) thinks the position

of the synaptic knot may be due to gravity. This does not seem to be true in Cypripedium, for the knot was found at all possible positions next the nuclear membrane in serial sections of the same ovary, and even in the same section. This was not only true for cross-sections, but also for longitudinal sections in which, since the ovary stands erect, gravity effects ought to be apparent. BURLINGAME (6a) has reached this same conclusion in his study of Ophioglossum.

SUMMARY

1. In Cypripedium two cells are formed by the mother cell, a wall not appearing in the second division, even in the rare instances in which the nuclei of both daughter cells divide. Two megaspore nuclei are used in forming the embryo sac, the Lilium type using four, and most angiosperms only one. The two megaspore nuclei in the sac of Cypripedium and the four in that of Lilium may be related to double fertilization.

2. Cypripedium has only four nuclei in the completed embryo sac. The Lilium type and Cypripedium have the fewest divisions from mother cell to egg reported among angiosperms. A comparison with the animal egg shows only one more division from the mother cell to the egg in Lilium and in Cypripedium than in the maturation of the animal egg.

3. So-called double fertilization is probably constant in Cypripedium. The primary endosperm nucleus (triple-fusion nucleus) is formed by the fusion of the polar, one synergid, and one male nucleus. Endosperm of four nuclei was found and the probability of other divisions taking place was noted.

4. In the presynaptic nucleus there is an evident pairing of the threads, probably of paternal and maternal origin. The gametophyte number of chromosomes is eleven, the sporophyte number is twenty-two, and the endosperm number is probably thirty-three. Distinct spirems were often found in all fusing nuclei, forming in one instance before contact. From these examples, the possibility of two spirems always forming in the sporophyte nucleus is suggested; this would secure the independence of the chromatin, and the fusing in synapsis would permit whatever exchange and mingling of parts there may be.

This research was carried on under the direction of Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN.

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EXPLANATION OF PLATES XXIV–XXVII

All figures were made with Bausch and Lomb camera lucida; *figs. 31* and *46* with Leitz no. 2 ocular and no. 7 objective; *figs. 61* and *62* with no. 4 ocular and no. 7 objective; all others with Leitz no. 4 ocular and B. and L. $\frac{1}{12}$ objective; details were filled in with a Zeiss apochromatic ocular and 2^{mm} objective.

The abbreviations used are as follows: *c*, chalazal daughter cell and nucleus; *e*, egg; *em*, embryo; *end*, endosperm; *g*, generative nucleus; *gc*, generative cell; *m*, micropylar daughter cell and nucleus; *meg*, megaspore nucleus; *p*, polar nucleus; *pe*, primary endosperm nucleus; *s*, synergid; *t*, tube nucleus; *ś*, male nucleus.

PLATE XXIV

FIG. 1. *C. spectabile*. Ovule with mother cell in synapsis.

FIG. 2. *C. parviflorum*. Mother cell with well-organized spirem showing distinct chromomeres.

FIG. 3. *C. spectabile*. Nucleus of mother cell, with a few threads showing beginning of pairing.

FIG. 4. *C. candidum*. Pairing of threads very evident throughout the nucleus, but only a few threads shown.

FIG. 5. *C. spectabile*. Synaptic knot forming; pairing of threads evident.

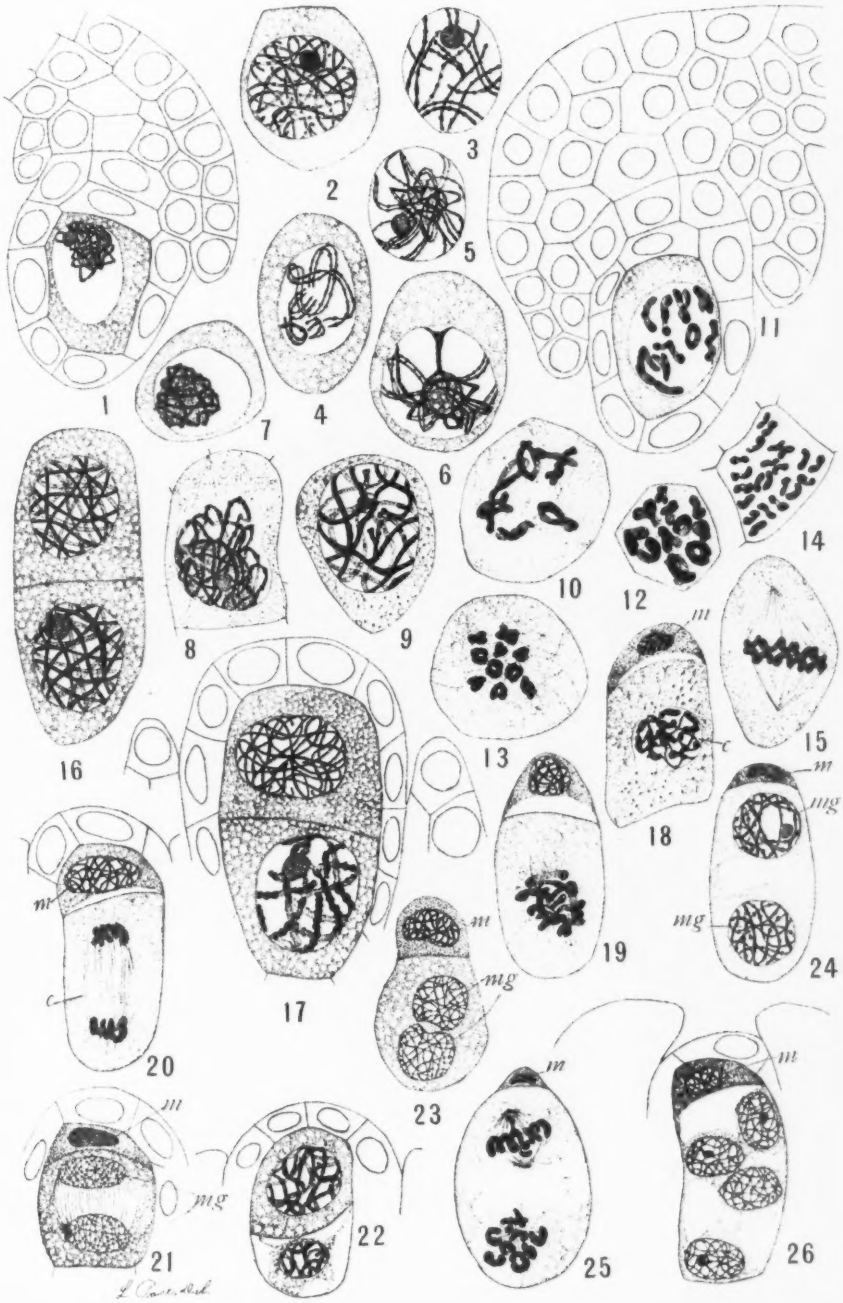
FIG. 6. *C. parviflorum*. Synaptic knot further advanced; threads in pairs and seemingly attached in places to nuclear membrane.

FIG. 7. *C. pubescens*. Synaptic knot complete.

FIG. 8. *C. spectabile*. Recovery from synapsis; lines of cytoplasm suggest multipolar spindle.

FIG. 9. Same. Shortening of thread; double nature evident at cut ends; lines of cytoplasm probably related to spindle formation.

FIG. 10. *C. pubescens*. Chromosomes formed.



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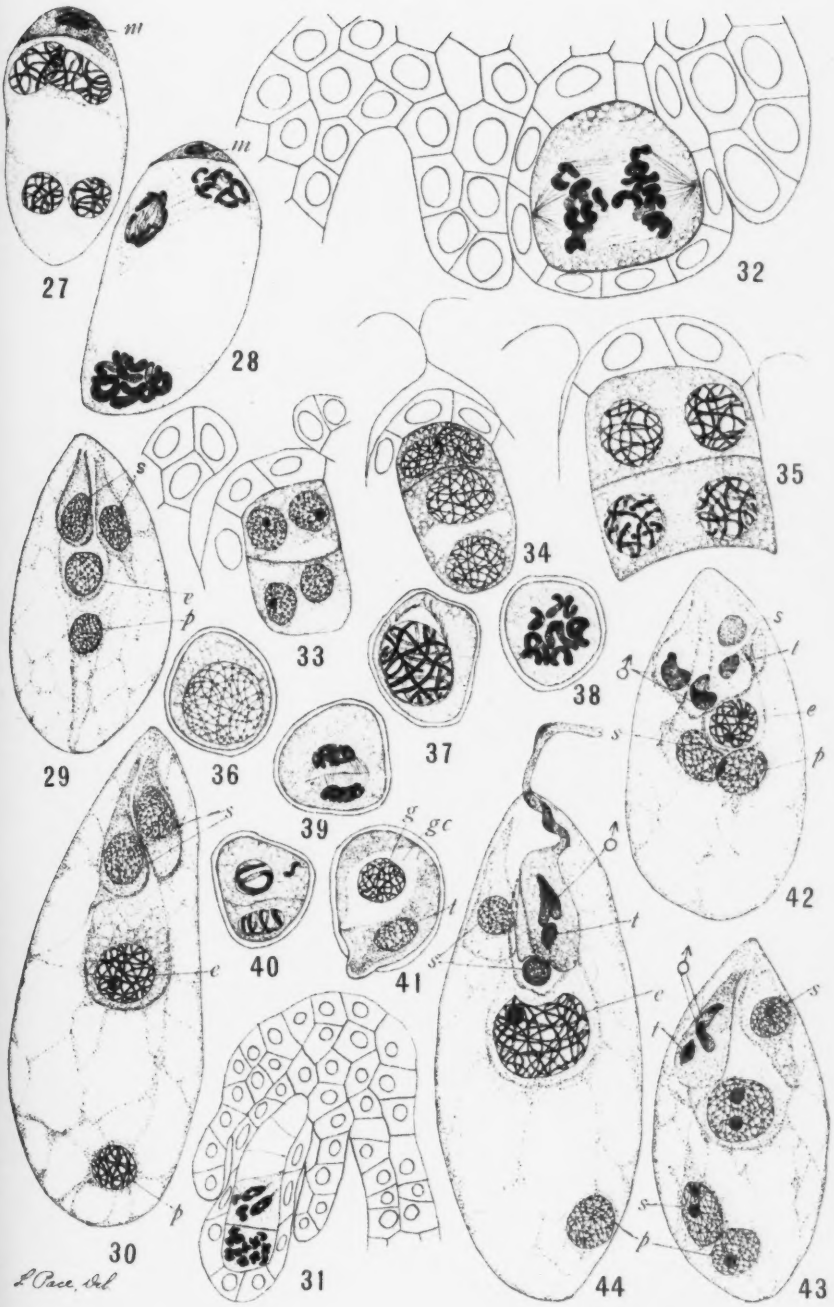

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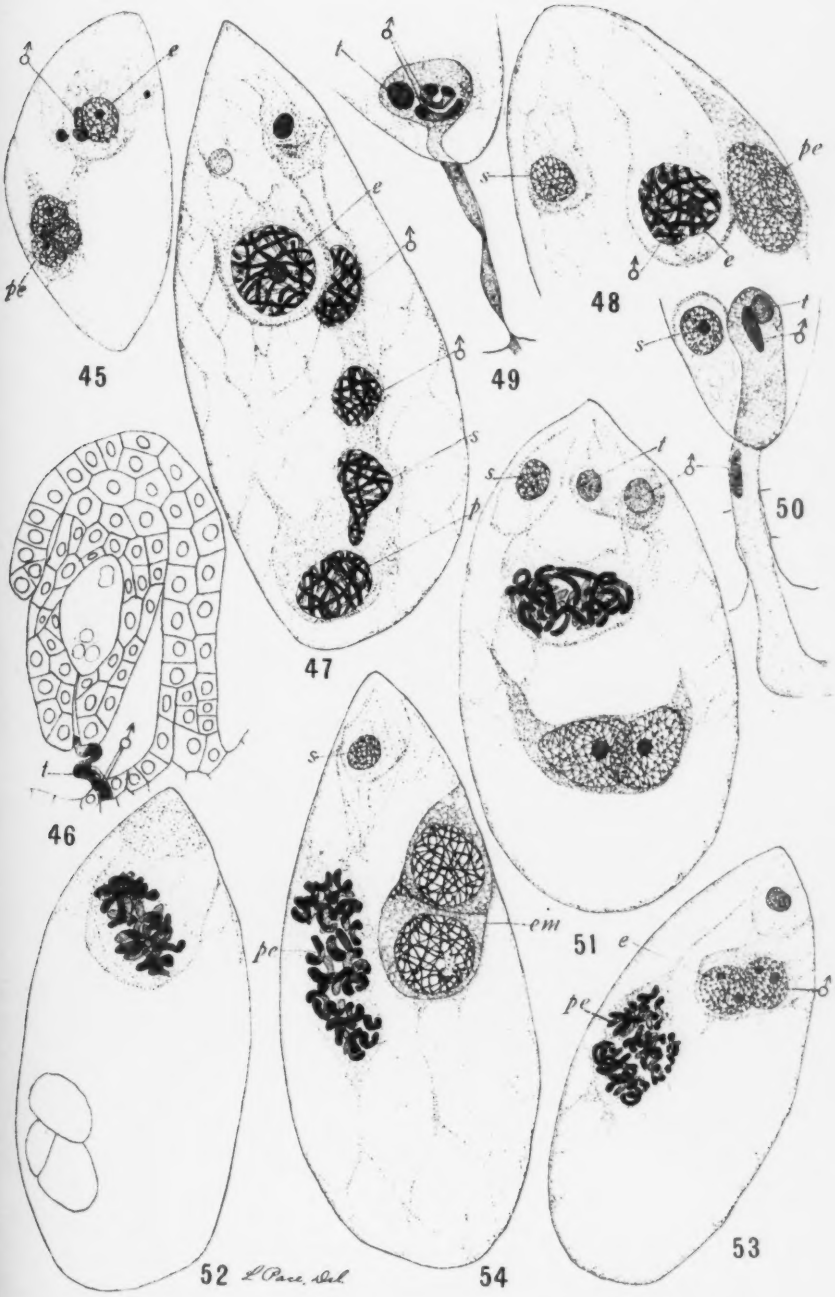

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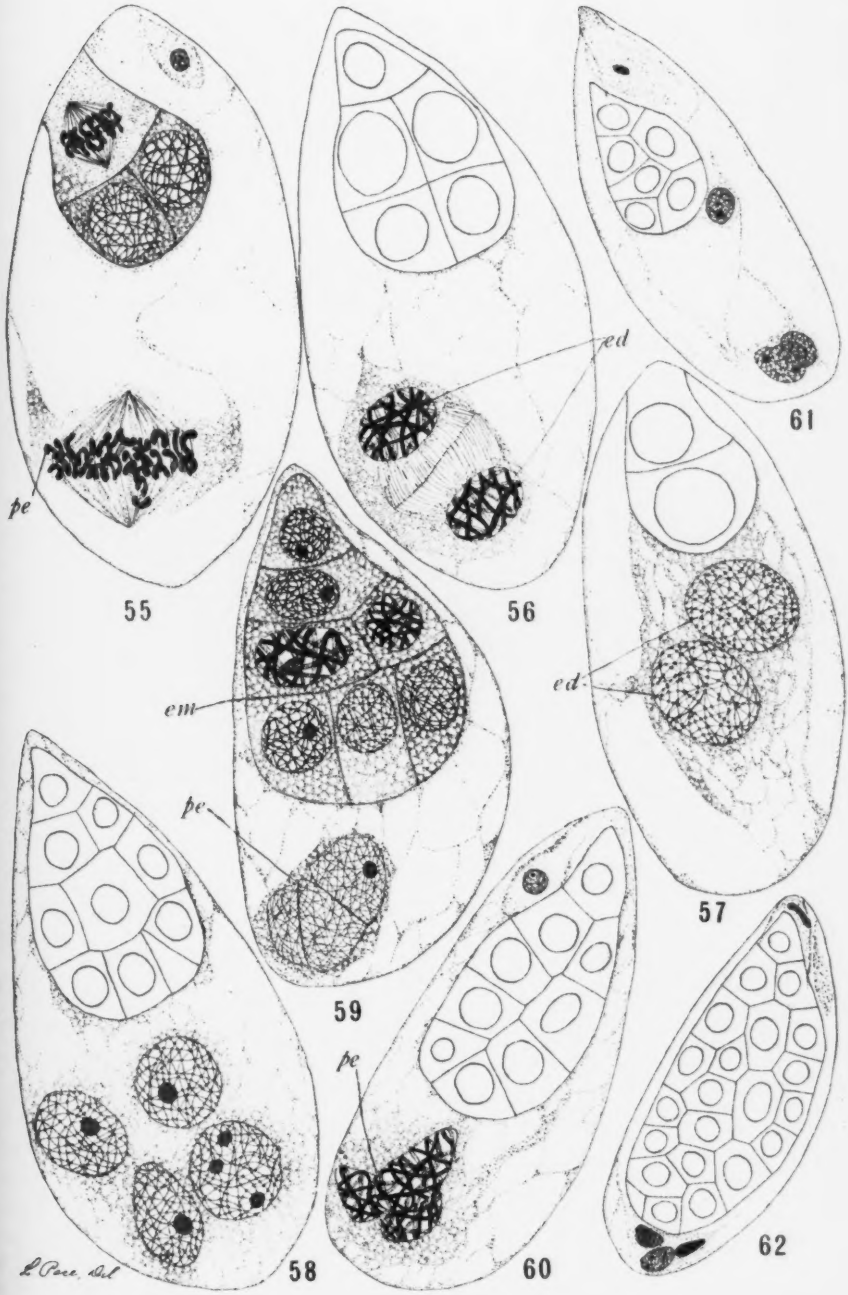

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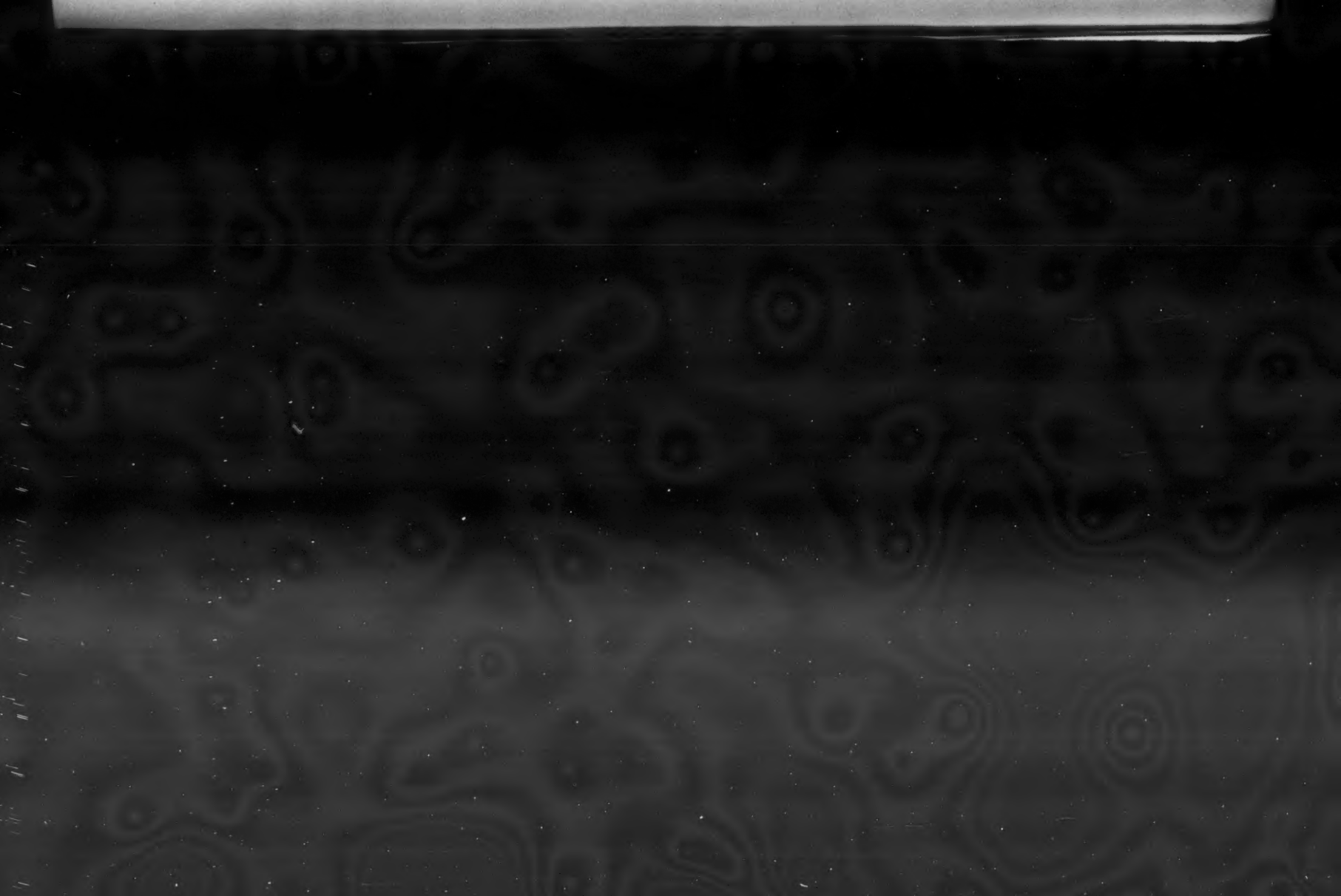

FIG. 11. Same. Ovule with mother cell in late prophase or in metaphase; origin of spindle indicated by lines of cytoplasm.

FIG. 12. Same. Eleven chromosomes.

FIG. 13. *C. spectabilis.* Eleven chromosomes.

FIG. 14. Same. Wall cell of ovule showing twenty-two chromosomes (sporophyte number).

FIG. 15. *C. pubescens.* Typical spindle of mother cell.

FIG. 16. *C. spectabile.* Daughter cells formed by division of mother cell.

FIG. 17. *C. pubescens.* Daughter cells, with chalazal nucleus farther advanced than the micropylar.

FIG. 18. *C. spectabile.* Suggestion of bipolar spindle.

FIG. 19. Same. Metaphase of second division, longitudinal splitting of chromosomes.

FIG. 20. Same. Telophase of chalazal daughter cell; no indication of wall.

FIG. 21. *C. parviflorum.* Division of chalazal daughter cell complete; remains of spindle, but no evidence of wall.

FIG. 22. *C. spectabile.* Micropylar daughter nucleus developing and the chalazal one disintegrating.

FIG. 23. *C. parviflorum.* Division shown in *fig. 21* completed; the sac slightly enlarged and containing two megaspore nuclei.

FIG. 24. *C. spectabile.* Early spirem for the division of the megaspore nuclei; micropylar daughter cell still recognizable.

FIG. 25. Same. Spindles for division of megaspore nuclei; micropylar daughter cell still persists.

FIG. 26. Same. Four-nucleate sac; micropylar cell still undivided.

PLATE XXV

FIG. 27. Same. Four-nucleate sac, the nuclei differing in size.

FIG. 28. Same. Nucleus at antipodal end of sac in late prophase; the other in late telophase.

FIG. 29. *C. parviflorum.* Embryo sac ready for fertilization, showing egg apparatus and "polar" nucleus (near center).

FIG. 30. Same. Another view of sac, showing polar nucleus near antipodal end.

FIG. 31. Same. Two mother cells.

FIG. 32. *C. spectabile.* Spindle of mother cell at right angles to its usual position.

FIG. 33. Same. Four megaspore nuclei of equal size; no walls at second division.

FIG. 34. *C. parviflorum.* Four megaspore nuclei, as shown in *fig. 33*, but the inner pair the larger.

FIG. 35. C. *spectabile.* Four megaspore nuclei; traces of spindle showing, but no trace of wall.

FIG. 36. Same. Pollen grain; early spirem for division to tube and generative nuclei.

FIG. 37. Same. Later stage; "cap" showing orientation of spindle.

FIG. 38. Same. Pollen grain showing eleven chromosomes.

FIG. 39. Same. Telophase; wall forming.

FIG. 40. Same. Wall completed; a chromosome omitted in the organization of one of the nuclei.

FIG. 41. Same. Pollen grain developing tube.

FIG. 42. *C. parviflorum.* Pollen tube within the embryo sac.

FIG. 43. *C. spectabile.* About same stage as *fig. 42*.

FIG. 44. Same. Earlier stage; tube within sac and one synergid below it.

PLATE XXVI

FIG. 45. *C. parviflorum.* Double fertilization.

FIG. 46. Same. Ovule with tube just entering, having passed from ovary wall to micropyle.

FIG. 47. Same. Spirems formed in all the fusing nuclei before contact.

FIG. 48. Same. Spirems of male and female nuclei farther advanced than of the nuclei to engage in the triple fusion.

FIG. 49. Same. Pollen tube entering sac; male nuclei elongated and curved.

FIG. 50. *C. spectabile.* Pollen tube unusually broad; one male nucleus some distance behind the other.

FIG. 51. *C. parviflorum.* Segmentation of egg; two groups of chromosomes.

FIG. 52. *C. spectabile.* Segmentation of egg; two groups of chromosomes.

FIG. 53. *C. parviflorum.* Male nucleus and egg just in contact; late prophase of primary endosperm nucleus, which shows thirty-three (approximately) chromosomes in three groups.

FIG. 54. Same. Two-celled embryo; primary endosperm nucleus in late prophase and showing three groups of chromosomes.

PLATE XXVII

FIG. 55. Same. Spindle forming for division of primary endosperm nucleus; three- or four-celled embryo.

FIG. 56. Same. Telophase of division of primary endosperm nucleus; wall forming.

FIG. 57. Same. Endosperm of two nuclei and a two-celled embryo.

FIG. 58. Same. Endosperm of four nuclei.

FIG. 59. Same. Embryo well advanced; triple-fusion nucleus still distinct but in the resting stage.

FIG. 60. Same. Older embryo; triple-fusion nucleus in spirem stage.

FIG. 61. Same. Embryo of several cells; nuclei of the triple fusion not yet in contact.

FIG. 62. Same. Much older embryo; probably a triple-fusion nucleus, but no evidence of division.

GERMINATION OF SEEDS OF WATER PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 104

WILLIAM CROCKER

Various botanists have noticed peculiarities in the germination of the seeds of water plants. MÜLLER[1] found that the seeds of Eichhornia and Heteranthera do not germinate without first being desiccated, and LUDWIG[2] demonstrated this for the seeds of *Mayaca fluviatilis*. In commenting upon this PFEFFER says:[3] "Nor is it certain whether BRAUN and MÜLLER are correct in assuming that previous drying is essential for the further development of Chlamydomonas or for the germination of the seeds mentioned." Dr. LAND, of this laboratory, informed me in the autumn of 1906 that he had made various attempts to secure seedlings of Sagittaria and Alisma for class use, but had always failed except in one trial with Sagittaria. In that case a number of seeds grew after being left for a long period on wet soil in a hot greenhouse. At that time I began looking into the cause for the failure to germinate and had arrived at the main conclusion of this paper when an article by FISCHER[4] appeared on the subject.

The main points of FISCHER'S paper may be stated briefly: The seeds of *Alisma Plantago*, *Potamogeton lucens*, *P. pectinatus*, *Hippurus vulgaris*, *Polygonum amphibium*, *Scirpus lacustris*, *S. maritimus*, *Sagittaria platyphylla*, *S. sagittifolia*, and *Sparganium ramosum* may be kept for years in water that is free from fermentation without germinating. If fermentation is set up in the water, germination soon begins. Germination can also be brought about, especially in Sagittaria, by subjecting the seeds to the action of bases and acids. FISCHER holds that the H^+ or OH^- ions act as stimulants on the

[1] See LUDWIG'S article below.

[2] LUDWIG, F., Ueber durch Austrocknen bedingte Keimfähigkeit der Samen einiger Wasserpflanzen. Biol. Centralbl. **6**:299, 300. 1886.

[3] PFEFFER, W., Physiology of plants (Eng. ed.) **2**:210. 1903.

[4] FISCHER, ALFRED, Wassertoff- und Hydroxylionen als Keimungsreize. Ber. Deutsch. Bot. Gesells. **15**:108–122. 1907.

dormant protoplasm of the embryo, arousing it to growth. He holds that the action is not on the coats, and adduces as evidence the facts that the seed coats are permeable to both water and compounds dissolved in it, and that a disorganization of the coats is brought about only by long exposure to such agents as concentrated H_2SO_4. He believes that the weak acids and bases used as stimuli could have no effect on the coats, and that in nature the germination is brought about by acid, formed in the decay of organic matter in ponds, which acts upon the dormant protoplasm.

I find that FISCHER is entirely wrong in assuming, first, that the protoplasm of these seeds is in a dormant stage; and, second, that a chemical stimulus is necessary to bring about germination. Likewise MÜLLER is wrong in assuming desiccation to be necessary for the germination of the seeds of Eichhornia. I find that the embryos of all seeds of water plants I have tested begin germination very readily when the ordinary conditions for germination are furnished them, and especially the one condition of sufficient water supply. In an article already published,[5] I have shown that cases of delayed germination or entire failure to germinate are generally related to the character of structures inclosing the embryo and not to dormancy of its protoplasm. In the paper cited I mention certain species of Iris that germinate only when the cap covering the embryo is removed, although the structures are permeable to water and the embryo imbibes water until it entirely fills the cavity it occupies. The water thus admitted is not sufficient to start growth, and the embryo lies in this semi-saturated condition. It is only when the limits to water absorption are removed that growth begins. Exactly the same thing occurs with the seeds mentioned by MÜLLER and FISCHER. Before discussing this point farther some facts about the ripening and harvesting of the seeds mentioned in the table below must be stated.

The seeds of Alisma, Sagittaria, and Typha all ripen above water, while those of Eichhornia and Potamogeton ripen under water, as do the seeds of many other water plants. The ripening under water is brought about by the flower stalks responding positively to gravity soon after fertilization. A large number of Eichhornia seed stalks

[5] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZETTE 42:265–291. 1906.

were gathered on October 1, while yet green, from one of the lagoons of Washington Park. Some of the green seeds were removed from the capsules and placed in distilled water, which was changed twice a day and kept at 23°C. Within a week twenty per cent. had germinated. A portion of the seed stalks were placed in distilled water repeatedly changed and kept at 23°C. Many of these seeds germinated while yet green and in the capsules. Still other seed stalks were kept in distilled water in an ice-chest at 6°C. None of these seeds germinated, but after three weeks many had ripened, as indicated by the hard brown coats. When the seeds with mature coats were kept at either 23° or 29° none germinated. Likewise seeds of *Potamogeton natans* and *P. pectinatus*, when gathered green and put into distilled water at 23° C. which was repeatedly changed, gave a considerable percentage of germination, while seeds allowed to ripen in the cold water of the ponds and then kept at 23° or 29° did not germinate.

If the real conditions demanded for the germination of the embryos of these seeds are to be determined, the embryos must be freed from any possible effect of the coats by carefully rupturing them without injuring the embryos. An experiment, the results of which are embodied in the accompanying table, shows conclusively the effect of the coats on germination, as well as the true condition of the embryos as to dormancy. Ripe seeds were used in this experiment. To guard against any possibility of acid formation by fermentation, the seeds of Potamogeton were entirely freed from the fleshy material surrounding the hard seed coat, all were sterilized in five per cent. formalin for eight minutes, and then washed thoroughly in sterilized distilled water. The coats of one-half the seeds of each species were broken, with sterilized instruments, at the point where the cotyledons naturally emerge from the coats. This is a very tedious process, because the seeds are so small (especially those of Sagittaria, Typha, and Alisma), and because great care must be taken not to injure the embryos. After this treatment the seeds were put into sterilized distilled water and placed in a bath at 29°C. During the first two days they were kept in total darkness and after that in diffuse light. Within an hour after the coats were broken the cotyledons projected considerably, on account of the rapid imbibition of water. In one

day germination was well started, as shown by the length of the cotyledons and their response to gravity. In two days the growth was very marked.

It might be urged that breaking the coats leads to increased oxygen supply and for that reason brings about germination. This is not at all probable for two reasons: first, increased oxygen pressures never bring about germination when the coats are intact; and second, these seeds require very little oxygen for germination. If the coats are ruptured, they will germinate if placed in water that has been previously boiled and covered with liquid paraffin. That the coats hinder germination by limiting the water supply is made evident by the fact that the cotyledon begins to project beyond the coat very soon after the latter is ruptured. In this experiment it seems impossible to justify the assumption that the protoplasm is in a dormant state or that the application of any external ions are necessary to start germination.

It is of interest to determine what structures surrounding the embryos limit the water absorption. In Sagittaria and Alisma there is an outer husklike exocarp and an inner hard endocarp. The removal of the exocarp did not increase the per cent. of germination, provided the endocarp was not injured in its removal. In Eichhornia the embryo is surrounded by a rather thick endosperm which is covered by a hard, fluted, brown seed coat. If the coat is broken at the side, it leads to a rather slow germination of over 50 per cent. of the seeds. If the coats are ruptured where the cotyledons naturally push out and where they lie very near the coats, nearly 100 per cent. germinate with remarkable promptness. This leads one to conclude that the hard coat chiefly limits water absorption, but that the endosperm too retards it. In the Potamogetons it is the hard stony coat that limits water absorption.

If the seeds of Sagittaria or Alisma are run through a coffee mill, set rather close, and are then placed in water, a large per cent. will grow. This breaks the seed coats without a very marked injury to the embryos. These seeds will also germinate after considerable time if planted in rich humus that is decaying by reason of abundant moisture and high temperature.

In the light of the work of MÜLLER and FISCHER two questions

Species	Condition of Coats	After 1 Day		After 2 Days		After 10 Days	
		Per cent. of germ.	Length of plantlets in mm.	Per cent. of germ.	Length of plantlets in mm.	Per cent. of germ.	Size of plantlets
Alisma Plantago.....	Entire	0		0		0	
	Ruptured	86	2–3	86	3–7	98	2 leaves
Eichhornia.....	Entire	0		0		0	
	Ruptured	96	2–4	98	4–7	98	2 leaves
Polygonum amphibium..	Entire	0		0		0	
	Ruptured	81	2–3	85	4–7	85	20–25mm
Potamogeton natans*...	Entire	0		0		0	
	Ruptured	42	3–5	51	5–8	51	20–30mm
Potamogeton pectinatus*	Entire	0		0		0	
	Ruptured	47	2–4	53	4–7	53	12–16mm
Sagittaria variabilis.....	Entire	0		0		0	
	Ruptured	92	2–3	92	4–7	92	2 leaves
Typha latifolia.....	Entire	0		0		0	
	Ruptured	85	2–4	89	4–8	89	2 leaves

* The low percentage of germination here is due to many of the seeds having no embryos.

demand answer. How does a period of desiccation bring about the germination of the seeds of Eichhornia as shown by MÜLLER, or of Potamogeton as shown by FISCHER? What was the rôle of the bases and acids in FISCHER'S experiments? My experiments indicate that drying followed by soaking causes a considerable per cent. of the coats of Eichhornia to crack along the flutings, while it causes the rupture of the coats of Potamogeton along two creases that lie at the convex side of the embryo. Just how the bases and acids work has not yet been determined. That FISCHER is wrong in assuming that they arouse the dormant protoplasm is evident, for I have shown that the embryos respond to ordinary germinative conditions almost, if not quite, as readily as any embryos to be found. The action that causes the germination must evidently be upon the structures surrounding the embryos. That H^+ and OH^- ions, as well as many others, may increase somewhat the rate of growth of the naturally rapid-growing embryos, is not at all improbable. The fact that the coats showed no visible change when treated with acids and bases does not indicate that the coats were not radically changed. I have found that the impermeable coats of many of the seeds of the Leguminosae are made permeable by soaking them in absolute alcohol, and yet no change visible with the microscope appears. Experiments are being conducted now to determine the

exact effect of acids and bases upon the seed coats and embryos of these seeds, as well as to determine in detail various other points connected with this problem.

I wish to emphasize again, as I have done already in the paper cited, the fact that delayed germination or failure to germinate is more generally due to seed-coat effects (limiting or entirely excluding water or oxygen supply) than to embryo characters, as has generally been assumed. On the other hand, in the same paper, I have shown that the failure of the seeds of hawthorns to grow under ordinary germinative conditions is due to embryo characters, and I have further stated that other seeds probably belong to this category. If seed coats play such an important part in failure to germinate, it is probable that spore coats act similarly in many cases. This hypothesis is now being tested.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

NOTES ON TWO CALIFORNIA NEMOPHILAS

NEMOPHILA MENZIESII var. **annulata**, var. nov.—Plants slender, prostrate, very brittle: cotyledons with oval blade and slender petiole: leaves rather less divided than in *N. Menziesii*, mostly 5-lobed, the upper greatly reduced but showing less tendency to become entire than in the variety *integrifolia* Parish: peduncles usually twice or more exceeding the leaves, often flexuous: flowers usually about or rather less than 1^{cm} across; calyx-lobes obtuse; corolla pale blue to almost white, with a deep-purple irregular ring above the scales, seldom dotted or hairy toward the center within; scales from 0.2 to 1^{mm} long, attached by one whole side or free at the tip (seldom as much as half free), ciliate with stiff bristles, which are often as long or longer than the scale is wide.

This variety is distinguished from the type by the greatly reduced size, lighter color, and peculiar markings of the corolla; the fewer-lobed, smaller leaves; the oval cotyledons; and the more delicate habit. From the variety *integrifolia* it is distinguished by the smaller size and the markings of the corolla; the lack of hairs within the corolla; the somewhat longer peduncles; the rather more divided leaves; and especially by the corolla scales (cf. note to *N. Menziesii integrifolia*, BOT. GAZETTE **34**:205. 1902).

This is the first Nemophila reported from the desert regions of California. It was found among rocks at Dead Man's Point, near Victorville, on the Mojave desert. The type collection is Hall and Chandler, no. 6769, and the type specimens are in the herbarium of the University of California.

NEMOPHILA MENZIESII var. **rotata** (Eastw.), comb. nov.—Very close to the variety *integrifolia* Parish, with which I united it in my Revision of the Genus Nemophila (BOT. GAZETTE **34**:194). The examination of more abundant material seems to justify the retention of the form as a separate variety. It differs from the variety *integrifolia* chiefly in the smaller flowers (usually less than 1^{cm} across), which are usually of much deeper blue and nearly or quite rotate. The sinuses of the corolla are comparatively deep and the lobes comparatively narrow. The scales are oblong-linear, deeply laciniate, and attached by the narrow base only. So far as seen, the corollas were not dotted toward the center, but were covered with long hairs at the base within.

The range of this variety seems to be restricted to the vicinity of San Diego, California, the plants of ORCUTT from Lower California cited by

Miss EASTWOOD in connection with the original description being probably *N. pedunculata* Dougl. This opinion was ventured in my revision, though at the time that was written the Lower California locality seemed to be far beyond the known range of *N. pedunculata*, which had not been found south of the Santa Inez Mts. Since then, however, I have found the species at Witch Creek, San Diego County, so that it may easily range into Lower California.—HARLEY P. CHANDLER.

BRANCHING SPORANGIOPHORES OF RHIZOPUS

(WITH ONE FIGURE)

Current texts agree in stating that the sporangiophore of *R. nigricans* bears a single sporangium. For example, SWINGLE states[1] that "each sporangiophore bears a single spherical sporangium." In a recent culture on bread, some two weeks old, two anomalous conditions were observed (*fig. 1*). In one case, by two successive branchings, one sporangiophore bore three normal sporangia. In the other case, by a single dichotomous branching, two sporangia were developed.—LEROY H. HARVEY, *Yankton College, Yankton, S. D.*

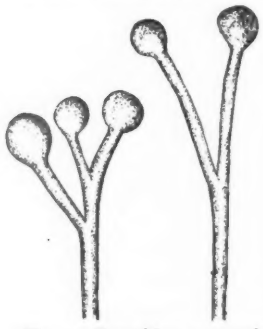

Fig 1.—Branching sporangiophores of Rhizopus.

AN UNUSUAL METHOD OF VEGETATIVE REPRODUCTION IN *DIONAEA MUSCIPULA*

(WITH ONE FIGURE)

In 1892 I described and illustrated an abnormal development of the inflorescence of Dionaea.[2] Two years ago I found an exactly similar kind of growth in a number of plants which had been kept in pots on a shelf next to the glass of a greenhouse with a southern exposure. In the axils of the bracts were found short vegetative branches, each with a number of perfect fly-traps (*fig. 1*), which closed when any of the six hairs on their upper surface were touched twice in succession. The response, however, was of the most sluggish character. The plants, when full grown, were rather crowded together by the arrangement of the pots, and whether this

[1] Bureau Pl. Industry Bull. 37. 1903. p. 15.

[2] HARSHBERGER, JOHN W., An abnormal development of the inflorescence of Dionaea. Contrib. Bot. Lab. Univ. Penn. 1:45–49. *pls. 5, 6.* 1892.

crowding induced the formation of the upper leafy branches I am unable to state. In the paper above mentioned, I suggested that "it might have been possible to have grown new individuals from the axillary vegetative branches, but the suggestion of this idea came after the plant had been killed and preserved in alcohol."

As a considerable abundance of material was provided by the abnormal growths produced two years ago, I cut off a number of the short leafy inflorescence branches and placed them in a sand bed used for the propagation of cuttings and covered with a hinged glass door. In ten days or two weeks after these interesting branches had been placed in the sand, they had developed, some one, others as many as four or five secondary roots, that had reached a length of one or two inches, when the plants were removed and placed in alcohol. The new plants, thus obtained by vegetative propagation, grew rapidly in the size of their leaves and were perfectly healthy and normal in structure. Thus, I verified the supposition made thirteen years ago that Dionaea can reproduce itself vegetatively by means of leafy branches proliferated in place of the inflorescence branches.—JOHN W. HARSHBERGER, *University of Pennsylvania.*

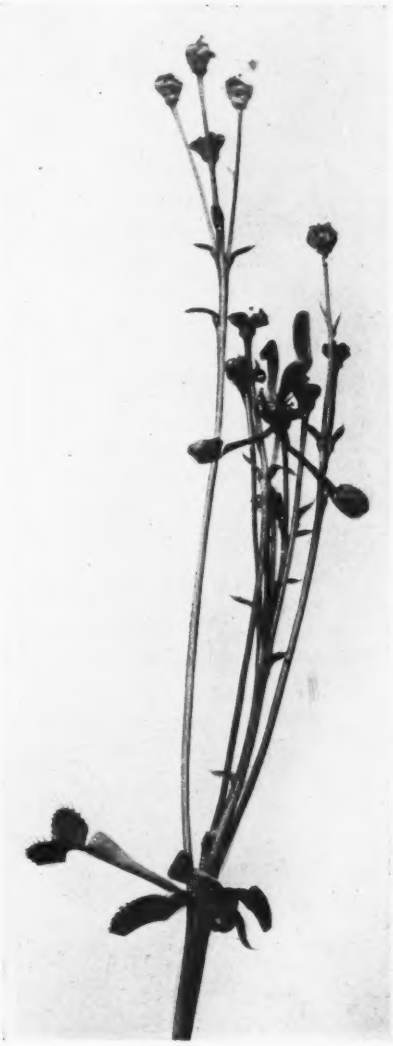

FIG. 1.—Dionaea muscipula.

CURRENT LITERATURE

BOOK REVIEWS

Handbook of trees

Many attempts have been made to bring into popular form such descriptions of our trees as would enable the amateur to recognize the various species at different seasons. It has remained for Mr. ROMEYN B. HOUGH to produce a book that adequately accomplishes this laudable purpose.[1] But it does much more; it brings to the forester, lumberman, cultivator, and botanist alike such a compact and comprehensive portrayal of the trees of the northern states and Canada as has never before been at his service.

As publisher of the well-known *American woods*, Mr. HOUGH has been much in the field and has thus had opportunity to make the notable collection of photographs which make this *Handbook* unique. He has not been satisfied with photographs of less than the highest quality. His pictures of leaves and fruits stand out, without distracting shadows, on a background ruled in 1-inch squares, showing at a glance the relative size, whether the original print is much or little reduced in making the fine half-tones for the book.

Each of the 208 species is illustrated by a full-page plate showing a branchlet with leaves and fruits, the latter usually dissected to show the seeds, and a twig in winter condition; a cut about 2×5 inches, showing a medium-sized trunk, with the normal appearance of the bark; and a small map of the United States and British America showing by shading the distribution of the species. In many cases there is in addition a cut about 2 inches square, showing a thin transverse section, magnified 15 diameters, which would often enable one to identify a doubtful piece of wood. These figures, admirably engraved and printed, are set on two facing pages, and in the small remaining space there is a letter-press description of the species, both diagnostic and general. At the end there are analytic keys and a glossary.

We cannot think of an item which would contribute to greater completeness. Everything that has been attempted seems to have been well planned and well executed. The basis of nomenclature is not stated; but synonyms in "recent works" are given. Of course much depends upon the accuracy of Mr. HOUGH'S identifications, but his long experience and the cooperation of other dendrologists ought to insure that. The book may be commended as indispensable for public and school libraries, for all students of trees, and for botanical laboratories. Considering the labor it represents and the wealth of illustration, the price is reasonable.—C. R. B.

[1] HOUGH, R. B., Handbook of the trees of the northern states and Canada east of the Rocky Mountains. Photo-descriptive. 8vo. pp. x+470. *figs. 498*. Lowville, N. Y.: The Author. $8.00.

Pavia memoirs

The tenth volume of the *Atti* of the botanical institute of the University of Pavia[2] precedes in publication the ninth, because the plates of an incomplete research are already printed and numbered for the ninth volume. Volume X, containing work dating from 1904 to 1907, opens with a portrait of FEDERICO DELPINO, a bibliography, and a brief dedication of the volume to him by his friend, the director, Dr. GIOVANNI BRIOSI.

There are several papers on plant diseases. First is an elaborate and well-illustrated account by BRIOSI and FARNETI of the white rust of the lemon, a serious disease in Sicily, due to some of the developmental forms of *Rhynchodiplodia Citri*, such as *Pseudofumago Citri*, *Cladosporium Citri*, *Hormodendron Citri*, etc. TURCONI describes a new fungus from Mexico, *Phyllachora mexicana*, parasitic on *Adolphia infesta* Meissn., the *chaquirilla*. FARNETI and POLLACCI describe a new mode of dispersal of phylloxera by hibernating larvae, inclosed in galls of peculiar form. FARNETI has a paper on a disease of rice, known in Italy as *brusone* and by a great variety of other names, which he ascribes to a single rather polymorphic fungus, *Piricularia Oryzae* Briosi & Cavara. It occurs also in Japan. It is transmitted by infected seeds and straw, and spores are distributed by wind and water. The parasite infests Panicum and Leersia also. BRIOSI details his rather hurried observations on the government nurseries of vines in Sicily, in which the disease *roncet* has appeared among the American stock destined to replace the vines destroyed by phylloxera. The disease is not threatening, but he recommends precautions. Besides these there are various short notes on fungus diseases.

There are several microchemical papers; one by CAZZANI is a critique of GORIS' work on esculin; another by POLLACCI suggests a better mode of testing for phosphorus in plant tissues. POLLACCI also reviews the history of the discovery of formaldehyde in plants and files his *caveat* as first discoverer in July 1899.

In physiology there are three papers. One is a short note by MONTEMARTINI, bringing evidence against JOST'S theory that the development of the leaf traces is due to stimulus from the growing organ above. A paper by the same author gives a résumé of the previous work upon the formation of proteids and reports the first results he obtained in a study of the effects of light on the process, which indicate that it is favorable thereto. POLLACCI, confirming his earlier conclusions, reports that plants emit hydrogen in light; but he also finds that they give it off in darkness, and that certainly cannot be related to photosynthesis. Nevertheless he maintains the reduction of H_2CO_3 by H_2 into HCOH+HOH+O.

The morphological papers include two brief notes by MONTEMARTINI, one on the origin of anomalous pitchers from the leaves of *Saxifraga crassifolia;* the other on a biological adaptation of the leaves of *Buxus sempervirens*, wherein he finds a mass of ice formed on freezing days between the lower epidermis and

[2] Atti dell' Istituto Botanico dell' Università di Pavia. Redatti da GIOVANNI BRIOSI. II Serie, Volume X. Imp. 8vo. pp. xxiv+361. *1 portrait. pls. 28* (20 colored). Milano: Tipo-Lit. Rebeschini di Turati E. C. 1907.

the mesophyll, which, he says, protects the leaf from further harm by cold and serves by retaining the water (ceded later to the stems) to facilitate the development of buds in spring!

The most voluminous morphological paper is one by BUSCALIONI and TRAVERSO on the morphological evolution of the flower in relation to the chromatic evolution of the perianth. They seek to show that the evolution of floral coloration is neither due merely to insect relations nor is it monophyletic. At least two lines are recognized, one characterized by the dominance of the xanthic series, the other by the cyanic. "Internal causes" primarily, then insect visits and "other factors," have been the agents in modifying the first flowers, which they assume to have been anemophilous—an assumption that needs defense. Of course "inherent causes" is simply a confession of defeat. HENSLOW'S theory (1893) came to their attention only after part of the work was printed; his book on *The origin of floral structures* is critically discussed in an appendix, and his theory mildly approved.

The volume closes with official reports of the work of the Royal Cryptogamic Laboratory of the Institute in 1904 and 1905. They show that it is doing good service for the country and the various researches indicate the activity and energy of the staff.—C. R. B.

Progress of botany

In the second part of the first volume of this admirable series, CZAPEK gives a résumé of the progress of our knowledge of the nutrition of plants since the publication of the first volume of PFEFFER'S *Physiologie*.[3] By his interpretation *Ernährungsphysiologie* covers even more than our blanket-word metabolism; for he discusses the mechanics of all the exchanges of material between the plant and the outer world, and the movement of water and foods within it, as well as the synthesis of foods, their assimilation, the non-plastic products, the ash constituents, enzymes and cytotoxins, respiration, and fermentation.

To do this within 114 pages would not be possible, were it not that the author can refer in many places to the summary already prepared in his *Biochemie der Pflanzen*. It must be remembered that a reporter sees things from a particular angle, and while we cannot always approve the point of view occupied by this author in surveying the field of research, we do recognize his synopsis as comprehensive and complete. It is especially useful in its inclusion of investigations carried on in eastern and southeastern Europe, that unfortunately are too often overlooked by the more western peoples, either through carelessness or unfamiliarity with the Slavic languages.

So much is included in CZAPEK'S summary that would hardly be expected even from the topics named, that it behooves every physiologist to read this paper and have it at hand for reference.—C. R. B.

[3] CZAPEK, FRIEDRICH, Die Ernährungsphysiologie der Pflanzen seit 1896. Progressus Rei Botanicae (ed. J. P. LOTSY) 1:417–532. Leipzig: Gustav Fischer. 1907. Per volume, *M* 18.

MINOR NOTICES

Gulf biologic station.—This station was established in 1903 by the state of Louisiana at the mouth of the Cameron River. The region is about at sea-level and practically treeless, the station itself being on a ridge running parallel to the sea and traversing a salt marsh. The plants of this very interesting locality have been published in a catalogue prepared by R. S. COCKS.[4] In addition to the list of species of the immediate vicinity, there are notes on certain species of the prairie region of southwestern Louisiana.—J. M. C.

Das Pflanzenreich.[5]—Part 29 contains the Erythroxylaceae by O. E. SCHULZ. After the usual preliminary account of literature, general characters, anatomy, geographical distribution, etc., the synopsis of the family is presented. Besides the monotypic genus Aneulophus, the family contains only the large genus Erythroxylum, which is credited with 193 species, 41 of which are described as new. The author breaks up the genus into 19 sections, to each of which a name is given.—J. M. C.

Key to trees and shrubs.—COULTER and DORNER[6] have published a convenient untechnical key to the genera of trees and shrubs of Indiana and the neighboring states, based chiefly upon leaf characters. A previous edition, now exhausted, was restricted to the forest trees, but the value of the present edition is much increased by including the shrubs.—J. M. C.

NOTES FOR STUDENTS

Mendelian inheritance.—DAVENPORT[7] in a lecture before the Washington Academy of Sciences discussed Mendelian inheritance in the light of his studies on poultry. After saying that "expectation has been so often realized that MENDEL's law has gained deserved fame as the most important law of inheritance yet enunciated," he proceeds to give a few non-conformable cases, and concludes that there must be some more inclusive law. This he calls the "law of potency," the gist of which may be given in his own words thus: "Between the two extremes of equipotency and allelopotency lies the great mass of heritable characteristics which when opposed in heredity exhibit varying degrees of potency." It is not clear why this should be called a law; it seems rather to be a denial that any law exists. Some cases similar to those cited have been found to conform with

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[4] COCKS, R. S., The flora of the Gulf biologic station. Baton Rouge: La. State Board of Agric. and Immigration, Bulletin 7. pp. 42. 1907.

[5] ENGLER, A. Das Pflanzenreich. Heft 29. Erythroxylaceae von O. E. SCHULZ. pp. 176. *figs.* 32 (297). Leipzig: Wilhelm Engelmann. 1907. *M* 8.80.

[6] COULTER, STANLEY, and DORNER, HERMAN B., A key to the genera of the native forest trees and shrubs of Indiana. pp. 24. Lafayette: The Authors. 1907. 20 cents.

[7] DAVENPORT, C. B., Heredity and Mendel's law. Proc. Wash. Acad. Sci. 9:179–188. 1907.

Mendelian expectation upon keener analysis of the characteristics involved, and it seems early for the formulation of a law to accommodate exceptional cases until hypotheses are exhausted for making them conform to laws now so fully demonstrated as those of MENDEL. There is no necessity for the assumption that there is an all-inclusive law of heredity, and it seems probable that there may be a number of more or less independent laws of greater or less inclusiveness which separately or conjointly may explain each single instance of inheritance. Some evidence exists that "variable potency" may represent a fact, but so far as the evidence goes, this fact is of much smaller significance than the segregation of pure gametes. Indeed it is conceivable that variations in potency may be due to several or many different causes, and that it does not represent a sufficiently unified series of phenomena to warrant its designation as a law.

COOK[8] in discussing DAVENPORT'S lecture attempts to classify various methods of descent, and limits "Mendelism" to cases of complete dominance, quite ignoring the feature of Mendelism now everywhere recognized as the most important, namely, the segregation of pure gametes. In the literature of Mendelism valid explanations of phenomena have been given belonging to most of COOK'S categories, and it seems not unlikely that Mendelian explanation will be found sooner or later for the greater part of the phenomena which COOK classes under polar inheritance. The classification as well as the whole paper is academic and represents thinkable conditions rather than actual ones. He attributes polar inheritance, except in the case of dimorphic and polymorphic species, to narrow breeding, but this assumption is as yet unsupported by experimental evidence. The paper is full of misconceptions and misstatements, the recklessness of which is in places startling and amusing. "Elementary species" (p. 206) are wrongly defined as the different kinds or castes of dimorphic or polymorphic species, and "heterozygote" (p. 211) is incorrectly limited to those heterozygotes which display novelties, i. e., characters not found in the parents. The tendencies of the author to construct a peculiar terminology to represent his thought rather than follow accepted usage is shown in the use of "conjugate" with the same meaning as the word "zygote," now universally adopted by experimenters in this field. Failing to grasp the possibility that any character may be made up of two or more factors, he is led to the startling conclusion (p. 220) that it is possible for germ cells to transmit characters for many generations without bringing or tending to bring them into expression, and that the Mendelian "laws of disjunction," "purity of gametes," "alternative inheritance," or whatever they may be called, become at once superfluous and inadequate.

His statements regarding mutations are all academic and mostly without any experimental support. Thus, he says (p. 199), "If the narrow breeding be carried on with persistence, mutative reactions toward greater diversity will appear, and these sudden deviations from an established heredity are even more

[8] COOK, O. F., Mendelism and other methods of descent. Proc. Wash. Acad. Sci. 9:189–240. 1907.

different than were the normally diverse individuals of the original species." Again (p. 220), "Mutative variations commonly obey MENDEL's laws." But none of the fully demonstrated mutations now known strictly obey MENDEL's law, though the reverse inference has been frequently made and probably with good cause, namely, that the Mendelian inheritance of a character indicates its origin by mutation. On p. 221 he says, "The general rule must be that new variant gametes conjugate with gametes of the unmutated parental type, and thus have from the first the reproductive status of Mendelian crosses." This is a good suggestion and should be kept in mind by students of evolution, as should also his discussion of the relation between the origin of characters and their effect in the modification of species; but the Oenothera mutants, the best known of all, breed true from the instant of their first appearance, and no instance is known in which a new form has been shown to be already a Mendelian hybrid at the time of its first appearance.

It is difficult to understand why COOK should say, "Mutation is not a period but a condition," since no one ever said or intimated that it is a period. It is neither a period nor a condition, but an act or the result of that act. He says, "Species have more essential evolutionary differences than mutations, though mutations are at the same time more definitely different." Yet the Oenothera mutants are recognized by excellent taxonomists as differing from each other both as to quality and degree, just as wild species differ. Other statements regarding the Oenotheras are not in agreement with published facts, as for instance his statement that *O. Lamarckiana* is dominant over *O. lata* to the extent of 85 per cent.—GEORGE H. SHULL.

The origin of angiosperms.—ARBER and PARKIN[9] have proposed a theory of the origin of the angiosperms, based on the recent development of knowledge in reference to living and fossil forms, especially the Bennettitales. Contrary to the ENGLER scheme, they do not regard such apetalous groups as the Piperales, the Amentiferae, and the Pandanales as representing primitive angiosperms, but rather as reduction forms from those possessing a perianth. The primitive typical angiospermous floral structure is claimed to have been an "amphisporangiate" (substituted for the commonly used terms "bisporangiate" or "ambisporangiate," as the proper antithesis of "monosporangiate") strobilus, in which the megasporophylls are above the microsporophylls and there is a well-marked perianth. Such a strobilus the authors call an "anthostrobilus," restricting "flower" ("eu-anthostrobilus") to angiosperms. A "pro-anthostrobilus" is an earlier form, such as is displayed by the Bennettitales, in which the megasporophylls are not closed, and the microsporophylls have not reached the real stamen form. This implies the existence of a direct ancestral group of the angiosperms, with a strobilus like that of the Bennettitales, and to this hypothetical group the

[9] ARBER, E. A. NEWELL, and PARKIN, JOHN, On the origin of angiosperms. Jour. Linn. Soc. London Bot. **38**: 29–80. 1907.

authors give the name "Hemiangiospermeae." To this hypothetical group the Bennettitales are related, but are specialized in their own way.

The living angiosperms most nearly related to the "Hemiangiospermeae" are the Ranales, especially the Magnoliaceae, whose probable primitive position has begun to force itself upon the attention of morphologists ever since WIELAND'S studies of Bennettitales; and from this same Ranales plexus the monocotyledons probably diverged. The monophyletic origin of angiosperms is maintained, but to the reviewer it seems altogether probable that while a simple strobilus, like that of Bennettitales, resulted in such a flower as that of the Ranales, a compound strobilus, like that of the Gnetales, may have resulted in such an inflorescence as an ament.

An inevitable suggestion is that the pteridosperms developed in the Mesozoic by two distinct methods: (1) by sporophylls aggregated into monosporangiate strobili leading to the modern cycads; (2) by both kinds of sporophylls massed into one amphisporangiate strobilus, as in Bennettitales.

The paper contains many interesting and suggestive details which cannot be mentioned here, and it brings together in every useful form views which have been working like leaven, but which had not been expressed.

Another paper dealing with the method of origin of angiosperms, rather than with their phylogeny, is that by COOK.[10] It is a theoretical discussion of the possibility of angiosperms arising directly from liverworts, such as Anthoceros, through the persistent aposporous development of the prothallia, which serve "as means of attachment for the young plant during its embryonic stages." "Apospory need not interfere with the formation of sex cells, nor with the continuation of truly sexual methods of reproduction." It seems that in this elimination of spores "mitapsis" is simply deferred to later generations of cells, in angiosperms being carried over into the aposporous female prothallium. From an Anthoceros capsule an angiosperm with two cotyledons could be derived; and then a many-leaved stem could be built up by the successive addition of "metamers." The elimination of megaspores in the life-history of angiosperms results in such new interpretations of structure that the reviewer must confess he is unable to follow the discussion. For example, "the part of the angiosperm which, in the present view, might correspond to the prothallus itself, is the nucellus. And even this relation would not be direct, for the nucellus of the angiosperms might not be homologous with the nucellus of the conifers and cycads, which, if current interpretations are correct, is more analogous to the placenta of the mammal than to an aposporous prothallus." Also, "the gymnosperms may be supposed to have the ovules and seeds naked because they are still borne in an endosperm which corresponds to the primitive, vegetatively functional prothallus, though it now remains attached to the much more highly developed double-celled structure which corresponds, in turn, to the capsule of the liverwort and the moss, the

[10] COOK, O. F., Origin and evolution of angiosperms through apospory. Proc. Wash. Acad. Sci. 9:159–178. 1907.

frond of the fern, and the leafy axis of the club moss." When revolutionary ideas are combined with evident lack of familiarity with the structures under discussion, it is no wonder that confusion is the result.—J. M. C.

Development of heterotypic chromosomes.—Two years ago MOTTIER published a preliminary account[11] of his views as to the development of the heterotypic chromosomes in pollen mother cells, and the full paper has just now appeared.[12] His paper consists of two parts: first, a statement of the results of his studies of five angiosperms (*Podophyllum peltatum, Lilium Martagon, L. candidum, Tradescantia virginica,* and *Galtonia candicans*); and second, a discussion of several cytological phenomena, reviewing the work of previous investigators and giving a purely theoretical account of the possible relationships of chromosomes to hereditary characters.

The few points which he has specially emphasized in his own studies on these five forms are as follows: (1) The resting nucleus of the pollen mother cell consists of a linin net, the ground matrix in which the chromatin is held. The chromatin is in the form of very fine granules of uniform size or in larger aggregations or clumps which are composed of smaller granules. (2) In synapsis he has not found a union of two spirems. (3) The loose or hollow spirem which has emerged from synapsis is of the double nature, which he believes to be due to a new longitudinal splitting that provides for the second division. (4) Segmentation of this loose or hollow spirem into chromosomes takes place during or following the second contraction stage. The second contraction consists in the arrangement of a large part of the spirem into loops that tend to radiate from a loosely entangled central mass of the thread. The loops are formed by the approximation of the parallel portions of longer turns of the spirem. Each loop represents a bivalent chromosome, each parallel part being a single chromosome. The two parallel parts or chromosomes are arranged tandem, or end to end in the spirem. (5) He seems to emphasize the point that the shortening and thickening of the spirem occurs, in the main, after segmentation of the spirem into chromosomes.

Taking his results as a whole, they confirm essentially the view already advanced by FARMER and MOORE, SCHAFFNER, and STRASBURGER. His theoretical discussion starts from this point: he has never found the number of chromosomes to be represented by prochromosomes in presynaptic stage; all identity of such bodies is lost. He thinks granules in the resting nucleus should be connected with smaller units, the pangens (following the terminology of DEVRIES); and with a purely theoretical consideration of the pangens and their relation to chromosomes and to heredity, the paper closes.—S. YAMANOUCHI.

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[11] MOTTIER, D. M., The development of the heterotypic chromosomes in pollen mother cells. BOT. GAZETTE **40**:171–177. 1905.

[12] MOTTIER, D. M., The development of the heterotypic chromosomes in pollen mother cells. Annals of Botany **21**:309–347. *pls. 27, 28.* 1907.

Resting buds as indices of ecological types.—RAUNKIAER[13] has regarded the world of vegetation from a somewhat new view-point, and has developed some ideas that seem of great value. Prevailing ecological classifications have commonly divided vegetation into xerophytic, mesophytic, and hydrophytic groups, in which the foliage organs have been the dominant element. RAUNKIAER thinks that the most rigorous season to which a plant is subjected is the one which should show the most critical ecological structures. Hence he proposes a new classification, based on resting buds and other organs that are most in evidence in rigorous seasons. On this basis five great plant classes are recognized: phanerophytes, whose buds are considerably above the ground (trees and shrubs); chamephytes, whose buds are slightly above the ground; hemicryptophytes, whose buds are at the ground level; cryptophytes, whose buds are hidden in the ground; and therophytes, whose buds persist only in seeds (annuals). The phanerophytes, especially, may be much subdivided: according to size into mega-, meso-, micro-, and nanophanerophytes; according to leaf-fall habit into evergreen and periodically deciduous; according to bud structure into forms with naked or scaly buds. Chamephytes may have stems that are erect in favorable seasons, or stems that are always horizontal. Cryptophytes are divided into geophytes, helophytes (marsh plants), and hydrophytes; geophytes are further subdivided into rhizome, bulb, root-tuber geophytes, etc. The author remarks on the distribution of these various types in relation to soil and climate. It is his idea that the classification of plant formations can be more readily and scientifically accomplished by the recognition of the above types than on other lines. The reviewer feels that the contribution is of great value, and that perhaps RAUNKIAER has given us the most practical classification of vegetation forms we yet have. It seems a pity, however, that the paper is cumbered with so many new terms. For instance, why say therophyte for annual? Too often good ideas are buried under a ponderous Greek or Latin terminology.—HENRY C. COWLES.

Antitoxic value of complete and of incomplete foods.—LE RENARD[14] has undertaken to ascertain how *Penicillium glaucum* can grow in such concentrated solutions of the salts of copper, and also how the resistance of the organism to the toxic salt is modified by varying conditions of nutrition. The maximum concentration of four salts of copper (sulfate, nitrate, chlorid, and acetate) which will allow germination in the presence of complete and incomplete foods has been determined. A complete food contains the eight essential elements according to the empirical formula $C_6H_{12}O_6 + NH_4NO_3 + MgSO_4 + KH_2PO_4 + H_2O$. An incomplete food is one whose corresponding empirical formula is deficient. Fully one-half of the paper is devoted to literature, general biology, and physiology of Penicillium, together with a long discussion of the nature of toxicity.

[13] RAUNKIAER, C., Types biologiques pour la géographie botanique. Bull. Acad. Roy. Sci. Lett. Danemark **1905**:347–437.

[14] LE RENARD, ALF., Essai sur la valeur antitoxique de l'aliment complet et incomplet. 8vo. pp. 1–211. Paris: J. Mersch. 1907.

The author draws thirty distinct conclusions, only a few of which can be noted here. A mineral salt used alone in normal or less than normal concentration does not increase the resistance of the fungus to copper salts, and therefore has no antitoxic value. Carbohydrates in the presence of a suitable mineral salt are antitoxic to an extent which for a constant quantity of that salt becomes zero at about centinormal for the aldoses, but reaches much lower for the ketoses and hexoses. The antitoxic action of a food seems to be correlated with a composition which includes a suitable carbon compound and a suitable mineral salt, united with an organic or a mineral acid. Such a combination the author designates a "complex" in which the toxin and the antitoxin are present in proportions which make a simple ratio representing a double compound (organo-metallic) which suggests by its composition and modifications the side-chain of EHRLICH. The germination of Penicillium in toxic solutions of copper is therefore to be attributed to the presence of such a complex. The paper is really an elaborate study of undoubted value, but the reviewer has not undertaken to digest the evidence for the conclusions enumerated.—RAYMOND H. POND.

Chemistry of fertilization.—LOEB'S address before the International Zoological Congress[15] is of general physiological interest. Summarizing all the experiments on artificial parthenogenesis, he says:

> It seems that the essential feature of the process of fertilization consists first in a liquefaction or hydrolysis or both, of fatty compounds, and second, in the starting of processes of oxidation in the right direction. These processes of liquefaction of fats and hydrolysis and oxidation form apparently the basis of the synthesis of nucleins. It is possible, but far from proved, that among the fatty compounds involved in the process of hydrolysis are the lecithins.
>
> These results are in harmony with the facts observed in the germination of oily seeds. The process of germination is an analogue to the starting of the development in the animal egg, inasmuch as resting cells are thrown into the process of cell division and this process is based upon the synthesis of nucleins. . . . . I think the chemistry of the germination of seeds is essentially the chemistry of nuclein synthesis, and I believe the method of starting this synthesis is essentially the same as in the fertilization of the egg. . . . . I am of the opinion that this mechanism of nuclein synthesis is the thread by which we can find a rational way through the maze of the otherwise bewildering mechanisms, characteristic of living matter; on one hand, the phenomena of growth, on the other, those of self-preservation. . . . . We must therefore conclude that the nuclei themselves or one of their constituents are the catalyzer for the nuclein synthesis or one phase of it. It is possible that the nucleus catalyzes only the phenomena of oxidation, and inasmuch as oxidations are the *conditio sine qua non* of nuclein synthesis, this would explain the autocatalytic effect of the nuclei upon this reaction.

It will be difficult to harmonize with this theory the germination of rice seed which, according to TAKAHASHI, germinate in the absence of oxygen, and the anaerobic growth of young shoots, described by NABOKICH.—C. R. B.

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[15] Science N. S. **26**:425–437. 1907.

Leaf structure and physical factors.—Most American ecologists have paid attention to the distributional rather than to the anatomical phases of their subject. For this reason the contribution of Mrs. CLEMENTS[16] has been particularly welcome. Few if any investigators have so thoroughly related leaf structure to definite physical factors. After a brief historical sketch, and a survey of the physical factors studied (light, water content of the soil, humidity, temperature), a detailed presentation is given of the characteristics of the mesophyll and epidermis of a large number of the plant species of various habitats in the Pike's Peak region of Colorado. The plants are divided into two classes, those confined to one habitat, and those that occur in two or more habitats (polydemic species). The latter seem to be the most numerous, and of course are the most interesting, as showing the range of specific variation. The various types of polydemic species are grouped so as to bring out graphically the effects of the various factors. The use of the word endemic for plants confined to one habitat, and mesophyll for a mesophytic leaf seem unfortunate in view of the long and wide use of these words in other senses. Among the more interesting of the results and conclusions, we may note that the lack of palisade cells is regarded as adaptational in many hydrophytes, but hereditary rather than adaptational in monocotyls; a typical xerophyte is regarded as having the chlorenchyma made up entirely of palisade cells; while light is regarded as the dominant factor in determining the palisade structure and close cell texture in xerophytes, dryness of air or soil is necessary for the extreme expression of this result. This paper is one that should stimulate many to carry on work along the lines of ecological anatomy.—HENRY C. COWLES.

Tomato rot.—The blossom end rot of tomatoes is again the subject of study. This is a widespread disease which has been studied repeatedly but without concordant results. The rot has been heretofore variously attributed to Macrosporium, Fusarium, Cladosporium, and to bacteria, while some workers have failed to find any parasites at all. The latest bulletin, by Miss SMITH,[17] describes the discovery, after very careful search, of small tufts of a colorless mycelium, protruding from intercellular spaces between the blackened walls into the still healthy tissue. Affected pieces of tissue in a moist chamber repeatedly developed an abundant growth of Fusarium. The affected tissue showed no bacteria. Pure cultures of the Fusarium were isolated and inoculations upon green fruit were successful, sometimes through the style but much more frequently through punctures in the epidermis. This disease does not develop well or at all upon old tomatoes, its damage being limited to young fruit. The writer correlates this fact with the increase of malic acid as the fruit increases in size; since her cultures prove that malic acid is extremely unfavorable to the growth of this species of Fusarium.

[16] CLEMENTS, EDITH S., The relation of leaf structure to physical factors. Trans. Amer. Mic. Soc. **1905**: 19–102.

[17] SMITH, ELIZABETH H., Mass. Agr. Exp. Sta. Technical Bull. 3. April 1907.

A bacterial rot of the tomato is also described in this bulletin. The bacteria were isolated from tomatoes which showed no sign of fungus growth. They were cultivated in pure culture and when reinoculated into the tomato fifty out of a total of sixty-seven inoculations produced the characteristic disease. There are thus two distinct diseases: a rot due to Fusarium and another rot due to bacteria.—F. L. STEVENS.

Root tubers of Dioscorea.—Some years ago QUÉVA described the vegetative organs of certain species of Dioscorea, and reached the conclusion that the tuberous body which occurs at the end of some of the roots represents an organ which has changed its nature from root to "something else." The matter was taken up by GOEBEL, who explains this peculiar body as an organ whose morphology lies between a shoot and a root. A much more simple and more natural explanation has recently been offered by LINDINGER,[18] who has studied *D. discolor*, and concludes that the roots do not change their morphological nature, but their function. The root consists of a slender, cylindric, basal portion, and a tuberous apical one, the former functioning as a nutritive, the latter as a storage root, which is also able to produce root-shoots. The anatomical structure of both regions is discussed, and it is interesting to notice that in the tuberous part the mestome strands are not arranged in a circle; that the inner mestome strands are collateral; and that, at least in some portions of the tuber, no endodermis is differentiated.—THEO. HOLM.

Secretory organs of Menispermaceae.—According to MAHEN,[19] these consist of ducts with tannin, ducts with caoutchouc, and secretory cells. Ducts with tannin occur in the cortex and pith of the stem, in the primary cortex of the root, in the parenchyma of the petiole, and in the midrib of the leaf. They are tubes of considerable length, and very often difficult to detect without tests for tannin; and are characteristic of certain species of Anamirta, Cocculus, Cissampelos, Burasaia, Calicocarpum, etc. Ducts with caoutchouc are known only in Tinomiscium, being found in all the vegetative organs as follows: in the stem, around the sclerenchymatic arches of the pericycle and in the pith; in the leaf, in midrib and petiole around the mestome strands. They are tubular and very thin walled. The latex is white and granulose, readily soluble in chloroform, but only partly so in absolute alcohol and ether. The secretory cells, observed only in *Abuta rufescens*, and containing an essence, abound in the stem near the sclerenchymatic pericyle on its outer and inner face.—THEO. HOLM.

A Linnean herbarium.—Although the herbarium of LINNAEUS went to London after his death, several other collections made by him and his pupils remained in Sweden, but have not been accessible until recently. In fact, it was not known

[18] LINDINGER, LEONHARD, Ueber den morphologischen Wert der an Wurzeln enstehenden Knollen einiger Dioscorea-Arten. Beih. Bot. Centralbl. **21**:311. 1907.

[19] MAHEN, JACQUES, Sur les organes sécréteurs des Menispermacées. Bull. Soc. Bot. France **53**:651. 1906.

where they were until the newly appointed curator of botany at the Swedish Academy, Professor C. A. M. LINDMAN,[20] discovered them among other bundles of plants stored away in "lumber rooms." These collections consist of the herbaria of CARL VON LINNÉ fil., ALSTROEMER, MONTIN, and SOLANDER, and contain many specimens named by LINNAEUS himself. These plants of LINNAEUS and his son, and from *Hortus Upsaliensis* during the lifetime of LINNAEUS, aggregate about 2000. They have been brought together as a "Herbarium Linnaeanum," and LINDMAN is now publishing a list of the species, arranged according to *Syst. Veget.* ed. 13 (1774) and *Suppl. Plant.* (1781).—THEO. HOLM.

Climate and plants.—H. VON GUTTENBERG[21] has made an anatomical and physiological study of the evergreen element of the Mediterranean flora, in part quite parallel to the studies which BERGEN has published in this journal and to some extent upon the same species. His work, however, was more extensive. It was done upon two islands, Lussin and Brioni Grande, near the Austrian coast of the Adriatic, and while his results as to transpiration do not always agree with BERGEN'S, their general drift is the same. The anatomical structure of the leaves is not of the extreme xerophilous type, because these plants must be able to take advantage of the more favorable conditions of spring and autumn, as well as to withstand the drought of summer. Thus, he finds the guard cells characterized by a special motility because of the "hinge" in the wall, so that they can prevent transpiration almost entirely by complete closure or allow it freely by wide opening. We may pe permitted some skepticism as to the perfection of this regulation, however.—C. R. B.

Anatomy of lianes.—FRIES[22] describes the anatomy of the stem and the aerial roots of a cucurbit, *Siolmatra brasiliensis*, with some notes on the mode of origin and form of the aerial roots of a species of Cissus, both occurring in the rain-forests of northern Argentina and southern Bolivia. Only two cases of the formation of aerial roots have been described among Cucurbitaceae, and in these the roots are small and known only in house-grown plants. But Siolmatra produces the long rope-like roots, reaching down from the tops of the highest trees, where the plant expands its foliage, to enter the ground and branch profusely. The most remarkable anatomical character of the stem is the presence of a secondary cambium in the pith, which produces groups of leptome and mechanical tissues on its inner face and groups of libriform cells on its outer face.—C. R. B.

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[20] LINDMAN, C. A.M., A Linnaean herbarium in the Natural History Museum in Stockholm. Arkiv. för Botanik Roy. Swed. Acad. Stockholm 7:no. 3. 1907.

[21] GUTTENBERG, H. VON, Anatomisch-physiologische Untersuchungen über das immergrüne Laubblatt der Mediterranflora. Engler's Bot. Jahrb. 38:383–444. *pls.* 7–9. 1907.

[22] FRIES, ROB. E., Morphologisch-anatomische Notizen über zwei südamerikanische Lianen. Bot. Studier tillägnade F. R. KJELLMAN 89–101. Upsala. 1906.

Driftwood from the arctic sea.—A large amount of driftwood has been examined by INGVARSON,[23] from Spitzbergen, Beeren Island, Jan Mayen, Greenland, and the mouth of Jenisei River. Among the conifers are species of Larix, Picea, Pinus, and Abies; while the deciduous plants belong mostly to Salix, Populus, and Betula. The structure of the trunks and roots is described and figured. The author reaches the conclusion that the polar current is a much more important factor in the transportation of driftwood in the arctic seas than is the gulf stream. The fact that seeds and fruits of various arctic plants have been found caught in the fissures of driftwood leads to the conclusion that the wide distribution of several arctic species may be due to such transportation.—THEO. HOLM.

A mutant of Leptospermum scoparium.—This shrub is very common in New Zealand, occupying vast tracts of usually barren country. The flowers are white, and the close-growing shrubs when in full bloom look as if densely powdered with snow. Pink forms are found now and then, but COCKAYNE[24] records the sudden appearance of a single plant with rich crimson flowers. This plant was taken possession of by a firm of nurserymen, and among the progeny obtained from the seed six more plants with crimson flowers appeared. The variation extends also to the size and color of the leaves, which are brownish instead of green.—J. M. C.

Linnaea borealis.—WITTROCK[25] has published thirteen mostly colored plates of Swedish forms of this species, and in the accompanying text has described about 160 forms. The vegetative organs are mentioned, but the author has made a special study of the shape and coloration of the corolla, which is beautifully illustrated. The American representatives are briefly described, and the following may be noted: *L. borealis longiflora* Torr. f. *angustissima* (Washington), f. *curticalyx* (Colorado), f. *minutifolia* (Vermont), f. *integerrima* (Alberta).—THEO. HOLM.

Monograph of Fraxinus.—LINGELSHEIM[26] has made a general study of Fraxinus as to its morphology (in the old sense), anatomy, geographical distribution, fossil forms, phylogeny, and classification. He recognizes twenty-seven species in § Ornus, nine of which are new; and thirty-two species in § Fraxinaster, four of which are new. The four new Fraxinasters are *F. rufescens* (Jaral 1315), *F. papillosa* (Townsend & Barber 354), *F. Pringlei* (Pringle 9417), all from Mexico, and *F. hybrida* from Florida (Curtiss 2321, Nash 941 and 1698).—J. M. C.

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[23] INVGARSON, FR., Om Drifverden i Norra Ishafvet. Köngl. Svenska Vet. Akad. Hdlgr. **37**:1. 1903.

[24] COCKAYNE, L., On the sudden appearance of a new character in an individual of *Leptospermum scoparium*. New Phytol. **6**:43–46. 1907.

[25] WITTROCK, V. BR., *Linnaea borealis* L., species polymorpha et polychroma. Acta. Hort. **4**:no. 7. 1907.

[26] LINGELSHEIM, ALEXANDER, Vorarbeiten zu einer Monographie der Gattung Fraxinus. Bot. Jahrb. **46**:185–223. *pl. 8.* 1907.

Flora Boreali-Americana.—It is generally conceded that ANDRÉ MICHAUX was not the real author of this work, and that it should be credited to RICHARD. CLOS[27] has brought the subject up again, and we learn that KUNTH in 1825 declared positively that RICHARD was the anonymous author of the work; and that RICHARD published very little himself, leaving to his friends and pupils the publication of many of his most important contributions. BEAUCHARDAT made a similar declaration before the faculty of medicine in Paris, in 1853.—THEO. HOLM.

Origin of asparagin in seedlings.—SCHULZE[28] has contemplated the work of others in connection with some of his own and offers in consequence the view that by the oxidation of the primary products of the dissociation of proteid (mono-amino-acids, hexone bases) ammonia is formed, and that the ammonia is then used in metabolism for the synthesis of asparagin and glutamin as the case may be. That enzymes are potent in the oxidation of the primary products mentioned he regards as probable.—RAYMOND H. POND.

Photosynthesis.—An excellent but all too brief résumé of the recent progress and present status of the problems of photosynthesis and the rôle of chlorophyll, given by KOHL[29] before the general meeting of the German Botanical Society in June 1906, has only recently been published in the *Berichte* (May 1907). It was too early to take account of the latest work of USHER and PRIESTLEY,[30] which would have modified radically some of its statements.—C. R. B.

Myxomycetes of Colorado.—BETHEL and STURGIS have begun the publication of a series of contributions under the general title "The Myxomycetes and Fungi of Colorado," the first number being a presentation of the Myxomycetes by STURGIS.[31] This first bringing together of the slime moulds of the state shows almost 100 species, representing 28 genera.—J. M. C.

Chromosomes of Oenothera mutants.—Miss LUTZ[32] has counted the chromosomes in the root tips of seedlings of *O. Lamarckiana* and of *O. gigas*, one of its mutants. The point of chief interest is that the number (probably 28) in the somatic cells of this mutant is double that found in the parental form.—J. M. C.

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[27] CLOS, D., La première flore de l'Amérique du Nord et Louis Claude Richard. Bull. Soc. Bot. France **53**:667. 1906.

[28] SCHULZE, E., Zur Frage der Bildungsweise des Asparagins und des Glutamins in den Keimpflanzen. Ber. Deutsch. Bot. Gesells. **25**:213–216. 1907.

[29] KOHL, F. G., Kohlensäure-Assimilation und Chlorophyll-Funktion. Ber. Deutsch. Bot. Gesells. **24**:(39)–(54). 1907.

[30] See BOT. GAZETTE **43**:144. 1907.

[31] STURGIS, W. C., The Myxomycetes of Colorado. Colorado Coll. Publ., Sci Series **12**:1–43. 1907.

[32] LUTZ, ANNE M., A preliminary note on the chromosomes of *Oenothera Lamarckiana* and one of its mutants, *O. gigas*. Science N. S. **26**:151, 152. 1907.

Structure of chloroplasts.—The examination of living and fixed chloroplasts of Chlorophytum and Selaginella convinces PRIESTLY and IRVING[33] that the chlorophyll occupies the peripheral layer, 1–3 μ thick, where it is held in the meshes of a network. The observations of TIMIRIAZEFF and NÄGELI on the splitting of the chloroplast when placed in a solution of low osmotic pressure are confirmed.—C. R. B.

Zymase from Aspergillus.—JUNITZKY[34] finds that the aerobically cultivated mycelium of Aspergillus always contains some zymase. He regards this result as favoring rather than as opposing the theory of the genetic connection of alcohol-fermentation with aerobic respiration.—RAYMOND H. POND.

Carex in N. W. America.—HOLM[35] has published an account of the genus Carex in northwestern America, the topics being (1) a synopsis of the species, (2) types characteristic of northwest America, and (3) the geographical distribution of the Carices of northwest America.—J. M. C.

Rate and period of growth of Polyporus.—EDGERTON[36] has found that the growth of *Polyporus lucidus* is exogenous and averages about 0.5^{cm} a day for the growing-period; and that the change in the development from stalk to pileus is a gradual process.—J. M. C.

Julianaceae.—The full paper dealing with this interesting new family of Mexican plants has now appeared.[37] The preliminary abstract for presentation before the Royal Society was noticed in this journal.[38]—J. M. C.

Aerenchyma.—WITTE[39] describes and figures the aerenchyma in *Lysimachia vulgaris* produced in stems in water, and records the production of this tissue in seven species of the Swedish flora.—C. R. B.

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[33] PRIESTLY, J. H., and IRVING, ANNIE A. The structure of the chloroplast considered in relation to its function. Annals of Botany **21**:407–413. *figs. 2.* 1907.

[34] JUNITZKY, N., Ueber Zymase aus *Aspergillus niger*. Ber. Deutsch. Bot. Gesells. **25**:210–212. 1907.

[35] HOLM, THEO., The genus Carex in northwest America. Beih. Bot. Centralbl. **22**[2]:1–29. 1907.

[36] EDGERTON, C. W., The rate and period of growth of *Polyporus lucidus*. Torreya **7**:89–97. 1907.

[37] HEMSLEY, W. BOTTING, On the Julianaceae: a new natural order of plants. Phil. Trans. Roy. Soc. London B **199**:169–197. *pls. 18–24. figs. 23.* 1907.

[38] BOT. GAZETTE **42**:236. 1906.

[39] WITTE, HERNFRID, Ueber das Vorkommen eines aërenchymatischen Gewebes bei *Lysimachia vulgaris* L. Bot. Studier tillägnade F. J. KJELLMAN 265–274. *figs. 10.* Upsala. 1906.

NEWS

MR. W. ERIC BROOKS has succeeded Mr. V. H. BLACKMAN in the department of botany of the British Museum.

MR. A. W. HILL, lecturer at Cambridge University, has been appointed assistant director of the Royal Gardens, Kew.

EDWARD W. BERRY spent the summer in collecting Mesozoic and Pleistocene fossil plants in Virginia and North and South Carolina.

MR. T. D. BECKWITH, Department of Agriculture, has been elected assistant professor of bacteriology and plant pathology at the North Dakota Agricultural College and Experiment Station, Fargo, N. D.

MR. J. H. SCHAFFNER, professor of botany at Ohio State University, has been granted leave of absence of one year to study in Germany. His work at the university will be cared for by Dr. A. DACHNOWSKI, University of Michigan.

A BIOGRAPHICAL SKETCH of the late MAXWELL T. MASTERS is published in Kew Bull. Misc. Inf. **1907**: 325–334, prepared by Mr. W. B. HEMSLEY. A bibliography is also published, not including contributions to the *Gardeners' Chronicle*, and containing 141 titles.

DR. TH. HERZOG, of Freiburg, has gone to South America for a stay of eighteen months, having been appointed botanist of a Portuguese commercial society organized to introduce "plant products" into Europe. His explorations will lie chiefly in Bolivia and the Amazon region, and in connection with his other work he hopes to obtain valuable collections of plants, and especially of mosses.

MR. C. F. BAKER, for three years past chief of the Department of Botany in the Estación Central Agronomica, at Santiago de las Vegas, Cuba, has been appointed curator of the Herbarium and Botanic Garden at the Museu Goeldi Pará, Brazil. All letters and packages should be addressed to him at that point after November 1, 1907. His especial function there will be the further development of the herbarium and garden at Pará, and the botanical exploration o some of the most interesting parts of the Amazon Valley.